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Editor
Tracy Elliot Hazen

Associate Editors

Albert Francis Blakeslee	Henry Allan Gleason	Louis Otto Kunkel
Cornelia Lee Carey	Alfred Gundersen	Michael Levine
Frank Earl Denny	George Tracy Hastings	Arlow Burdette Stout
Alexander William Evans	Marshall Avery Howe	Sam F. Trelease

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Erratum

Page 489, 16th line from bottom, for '**Hypochnus** *sublitis*' read '*Hypochnus subtilis*.'

The morphogenetic relationships between cell and organ in the petiole of Acer

EDMUND W. SINNOTT

(WITH FIVE TEXT FIGURES)

Among the various problems in the field of plant morphogenesis, none perhaps exceeds in interest and importance the question as to the relationship between the size and shape of a given organ and the size and shape of the cells which compose it. Is an organism to be regarded as the resultant of the more or less independent morphogenetic activities of its constituent cells, or are the form-determining factors super-cellular in the sense that they operate on living tissue in the mass, regardless of the characters of the particular cellular units into which it may be divided? The chief issue between the cell theory and the organismal theory is joined at this point, and in view of the increasing interest in experimental morphology and developmental problems in general, it is rather surprising that the matter has not received more adequate investigation.

Since the early work of Sanio and Gregor Kraus, cell size has been studied by many botanists, particularly in its relation to body size, specific differences, nanism, etiolation, and nuclear constitution, but the conclusions in most cases have been drawn from a rather limited body of evidence and are often conflicting in their bearing on morphogenetic problems. A comprehensive survey of the literature on cell size is impossible here, but there are a number of papers of particular interest in this connection which should be mentioned briefly. Amelung (1893) found practically no difference between cell size in leaves of diverse sizes growing on the same plant, and little between different individuals of the same or related species. His conclusion that body size is chiefly determined by number rather than by size of cells was accepted and emphasized by Sachs (1893). Sierp (1913), in a careful and extensive survey, found that the facts are not quite as simple as this, but that cell size may vary markedly between two plants of the same species and between different organs or regions of the same individual, and that it is influenced to some extent by environmental conditions. There is probably, he thinks, an average cell size characteristic of each plant but it is difficult to determine without an extensive series of measurements. Obaton (1922) observed that small size in the leaves of trees is due to fewer rather

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than smaller cells. Kraus (1869) had reported that etiolation results in a marked increase in cell size, but Brotherton and Bartlett (1918), as the result of a more detailed analysis, found that the increase in length due to etiolation was associated with a considerable increase in cell number as well as in cell size. The relation of cell characters to dwarf habit has been studied by a number of investigators. Gauchery (1900) observed various histological differences between normal plants and dwarfs, the latter often having smaller cells. Sierp called attention to the existence of three types of dwarfs: those with cells smaller than normal, those with cells of about normal size, and a few with cells actually larger than normal. Oehm (1924) found that cell size rather closely paralleled plant size in a series of four forms in *Hedera*. Bailey and Tupper (1918) and others have reported considerable variation in the length of wood cells associated with plant age, vigor of growth, and other factors. A relation between cell size and chromosome number has been observed by many workers.

These studies have shown that cell size is much more variable than some of the early investigators supposed, but the morphogenetic implications of the results have been distinctly meager. In the great majority of cases, the observations have dealt chiefly with epidermal tissues and the leaf blade. General conclusions based on data from these sources are open to serious question, as will be shown later. There is need for many thorough studies dealing with various tissues and parts of the body before we shall be able to evaluate the rôle played by cell size in determining the size of the individual itself.

The situation is even less satisfactory in the problem as to the relation between cell characters and organ shape. To be sure, if cellular dimensions are relatively constant, differences in shape must be due merely to differences in rate of division in different directions, but the established variability of cell size certainly raises the question as to whether this may not also affect the shape as well as the size of the structures produced. Only a few investigators have studied the cellular basis of shape differences. Among them is Miss Tenopyr (1918), who found that in leaves differing markedly in shape, both on the same plant and in different plants of closely related species, neither cell size nor cell shape was concerned, but that the leaf shape differences were due entirely to greater cell numbers in certain dimensions than in others, resulting from different rates of cell division. Lehmann (1926) found that in potatoes, although there is a clear correlation between the size of the tuber and the size of the constituent storage cells, differences in tuber shape are associated with the presence of more cells in certain dimensions than in others, and are not due

to differences in cell size or shape. Sinnott and Durham (1929) also observed that in squash fruits differing radically in shape the cells were essentially alike.

The purpose of the present investigation is to make a detailed study of cell size and shape in the various tissues of a plant organ which is itself variable in these respects in order to determine as definitely as possible the relations which may exist between cell traits and organ traits.

MATERIALS AND METHODS

Material for a study of this problem in its simplest form must fulfil three conditions: it should possess genetic uniformity, marked histological differentiation, and a wide range of variability in shape. The first condition is satisfactorily met by the multiple but morphologically equivalent organs of a single plant individual, such as leaves and flowers, which are presumably identical genetically. Both these organs consist largely of primary tissues, and the complications introduced by cambial acitivity, such as are often present in the stem, are avoided. Leaves have several advantages over flowers or floral parts, since they are much more abundant and accessible, have a greater variety of tissues, and are more variable in size and shape. The leaf has consequently been widely used in studies of this nature, but in almost every case the blade has been the organ investigated. Much more favorable material, however, seems to be presented by the petiole, since it is less specialized physiologically, has a greater range of tissues, and is considerably more variable in its dimensional ratios.

In the present study thirty pairs of leaves from a single tree of *Acer saccharum* Marshall were used, constituting the entire foliage of eleven shoots. Twigs nearly or quite horizontal in habit of growth were chosen in order to take advantage of the great range in variability consequent upon the anisophylly induced by such orientation. The position of each leaf on the shoot was recorded and the blades as well as the petioles were carefully measured. Blade area was determined by outlining it on standard-weight paper, cutting out, and weighing the cut-outs. Blade thickness was measured by a micrometer caliper at two points symmetrically placed on both sides of the midrib and free from large veins, the two measurements being averaged. The length of the petiole was measured directly, and its diameter in the mid-region determined by a micrometer caliper. From these data the area and volume of the blade, the cross sectional area of the petiole, the volume of the petiole, and the shape index (length /diameter) of the petiole, were calculated.

Two short pieces were cut out from the middle of each petiole, and killed and imbedded. From these, transverse and median longitudinal sections were cut. The transverse section shows a circle of bundles, usually eight in number, which form a closed ring roughly circular in outline (fig. 1), so that a structure somewhat resembling that of a stem is produced. Disregarding exact morphological equivalency, we may for convenience speak of this as the 'vascular cylinder,' surrounding a 'pith' and being surrounded by a 'cortex.' At a low magnification the transverse section of each petiole was drawn with a camera lucida and the vascular cylinder outlined. From this, the diameters of the cortex and vascular cylinder were determined.

Under a high magnification a large group of cells from several portions of the transverse section, chosen along the line *A*–*B* in figure 1, were carefully drawn in outline by camera lucida. These were (1) a portion of the epidermis and the two successive hypodermal layers of the cortex immediately underneath it; (2) the phloem fibers of the abaxial central bundle; (3) the entire group of vessels of this bundle; and (4) the central portion of the pith. Measurements were made of the drawn outlines and from these the actual dimensions were readily computed. It is believed that this method is somewhat more rapid and accurate than the use of a micrometer eyepiece, and it has the further advantage of providing a permanent record of the data. The transverse dimensions of the cells of the epidermis, the first and second hypodermal layers, the phloem fibers, the vessels of the xylem, and the cells of the pith were thus measured. In most of these tissues there was considerable apparent difference in the diameters of the various cells. Some of this was real, but much of it, particularly in the vascular elements, was evidently due to the fact that the width varied markedly according to the level at which the cell was cut. To standardize the measurements somewhat and to eliminate most of the cases where the section was not through the widest diameter of the cell, only half of the total number of cell outlines in a group, comprising in every case only the widest ones, were chosen for measurement. Each cell was measured on its longest diameter, and again at right angles to this (most of the cells were nearly isodiametric) and the two determinations averaged. From this average the actual diameter of the cell in microns was determined and its cross sectional area computed. The diameters of all the cells measured in a given tissue group in each petiole were averaged, and thus an average cell diameter for each cell group was found for each petiole; and the average cell cross-sectional area was computed in the same way.

The longitudinal sections were studied in a similar manner and under the same magnification, and the average cell length for each tissue de-

termined in every petiole. Because of the long and tapering end walls of the fibers and vessels it was found impossible to obtain accurate determinations for these. The cells of the pith and cortex, however, with their end walls rather sharply cut at right angles to the axis of the petiole, were readily measured. The epidermal cells, on account of the fact that many of them were not rectangular in shape, presented more difficulty, but by measuring the total length of a number of long series of cells and counting the cross walls visible in it, an accurate average was determined. A surface view of the epidermis showed the elongate tapering primary cells divided transversely into smaller ones, to which Brotherton and Bartlett have called attention. It is these ultimate units which were here measured.

Fig. 1. Diagram of cross section through petiole of *Acer*. In the tissues where cell division was measured (epidermis, first and second hypodermal layers, phloem fibers, vessels, and pith) the location and approximate extent of the area studied are indicated by the portions in which the cells are outlined.

By multiplying the average cross sectional area of a given tissue group in each petiole by the average cell length of this same group, a cell volume characteristic for this tissue and petiole was computed. This of course is not truly an average cell volume, since the cells measured for width were not the same ones that were measured for length, but they were essentially comparable, and the volume figures are doubtless reasonably accurate.

By dividing the average cell length (where this was available) by the average cell width for each tissue, a cell shape index characteristic of that tissue was determined for each petiole. By dividing the average cell length into the entire petiole length the number of cells lengthwise of the petiole could also roughly be calculated for each tissue.

Thus the size and shape of each petiole and the size and shape of the more important types of its constituent cells were found. From the data thus derived, determinations of comparative variability of petiole and cell characters, and of the correlations between them, were readily made.

RESULTS

Petiole characters

The groups of petioles varied widely both in dimensions and shape. In length they ranged from 1.6 to 22.5 cm., with a mean of 8.92 cm. and a coefficient of variability of 57.62 per cent; and in diameter from .63 to 2.59 mm., with a coefficient of variability of 28.98 per cent. This greater

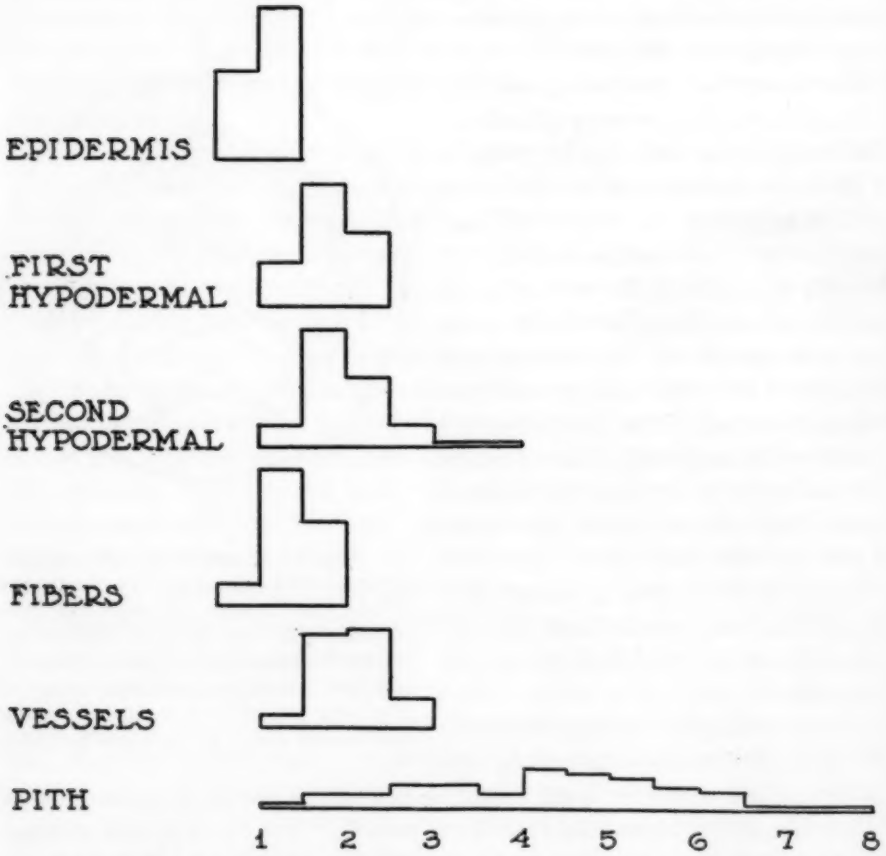


Fig. 2. Graphs showing distribution of the average cell diameters per petiole in the six tissues studied. Each unit is .01 mm.

variability of length has been found to hold in a much more extensive series of measurements, involving 1000 petioles, and is apparently due to a difference between longitudinal and transverse growth, both as to the manner in which they are brought about and the effect upon them of environmental factors. With these dimensional differences it was to be expected that the range in petiolar volume would be great, and it was

found to extend from 5 to 684 cubic millimeters, with a mean of 171 cu. mm. and a coefficient of variability of 108.18 per cent. The shape index (ratio of length to diameter) is also highly variable, extending from 20.5 to 153.1, with a mean of 62.9 and a coefficient of variability of 52.15 per cent. In diversity in size and shape, therefore, the petiolar material studied was admirably adapted to the problem at hand.

Cell characters

The most important fact brought out by a comparative study of the cell characters is that the various tissue systems not only differ

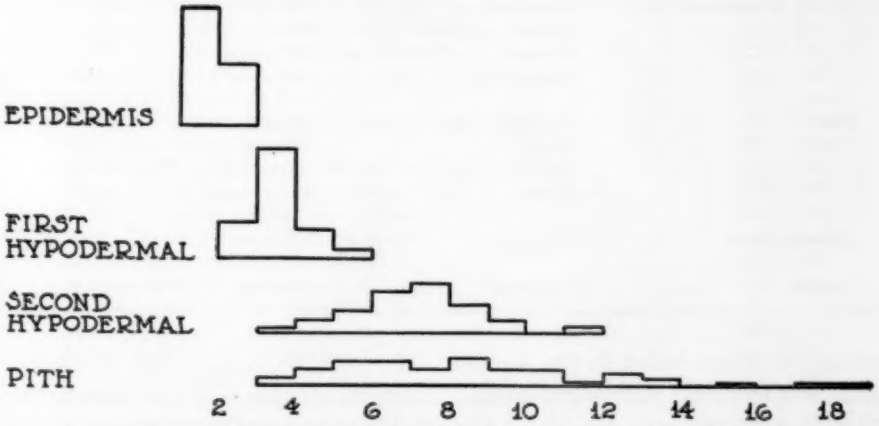


Fig. 3. Graphs showing the distribution of the average cell lengths per petiole in the four tissues studied. Each unit is .01 mm.

markedly in the size and in the shape of their cells, but also in their relative variability with regard to these two traits. The facts are set forth in detail in table 1, and the distributions for cell diameter and cell length are shown graphically in figures 2 and 3. The single variate in each case is the average determination for each petiole.

There is obviously an enormous difference in dimensions between the cells of the epidermis and those of the pith, the latter averaging nearly one hundred times as great in volume as the former, with the two outer cortical layers intermediate in size.

In diameter there is a rather slight increase in size as one passes from the epidermis through the cortical layers, with a sharp rise in the pith. In length, the change is much more rapid, but in all cases it is progressive from the outer layers of fundamental tissue to the inner ones.

In shape, the situation is somewhat different. There is little difference between the epidermis and the first hypodermal layer, but a sharp in-

TABLE 1

Biometrical constants for cell size and shape in various tissues in the petiole of Acer saccharum

TISSUE	CHARACTER	MEAN	COEFFICIENT OF VARIABILITY
			per cent
Epidermis	Diameter	.010 mm.	12.2
	Length	.018 mm.	16.8
	Volume	1890 cub. μ	43.4
	Shape	1.85	23.9
First hypodermal layer	Diameter	.019 mm.	19.9
	Length	.035 mm.	17.8
	Volume	10,280 cub. μ	34.4
	Shape	2.08	24.2
Second hypodermal layer	Diameter	.019 mm.	25.9
	Length	.072 mm.	23.2
	Volume	25,700 cub. μ	67.4
	Shape	3.99	22.9
Pith	Diameter	.043 mm.	33.8
	Length	.086 mm.	38.6
	Volume	183,000 cub. μ	79.8
	Shape	2.03	45.7
Phloem fibers	Diameter	.014 mm.	18.6
Vessels	Diameter	.021 mm.	16.2

crease in shape index in the second. The pith, in turn, is not markedly different from the outermost layers. These results are of course due to the fact that, in the pith, length and width increase together, whereas in the second hypodermal layer the cells have reached almost the length of those in the pith but have increased but little in diameter. In the cortex as a whole, the length of the cells is approximately as great as in the pith but their width is rarely as great.

Even more notable are the differences between the tissues in their variability. In every trait the epidermal cells are very much less variable than the pith cells, and the hypodermal layers are generally intermediate. Evidently there are factors which operate to keep the size of the epidermal cells essentially constant, and these factors are of progressively less effect in the deeper layers of the fundamental tissue. The significance of this fact in the problem as to the interrelationship between cell characters and organ characters is obvious.

Relations between cell and petiole characters

The various correlation coefficients which have been determined between cell and petiole characters have all been brought together in table 2.

TABLE 2

Coefficients of correlation between cell characters and petiolar characters in Acer saccharum

CHARACTERS CORRELATED	COEFFICIENTS
Petiole volume:epidermal cell volume	.099 ± .104
Petiole volume:1st hypodermal cell volume	.524 ± .076
Petiole volume:2nd hypodermal cell volume	.599 ± .067
Petiole volume:pith cell volume	.811 ± .038
Petiole diameter:epidermal cell diameter	.011 ± .091
Petiole diameter:1st hypodermal cell diameter	.633 ± .055
Petiole diameter:2nd hypodermal cell diameter	.637 ± .054
Petiole diameter:phloem fiber diameter	.836 ± .027
Petiole diameter:vessel diameter	.552 ± .063
Petiole diameter:pith cell diameter	.927 ± .016
Cortex diameter:epidermal cell diameter	.190 ± .092
Cortex diameter:1st hypodermal cell diameter	.707 ± .046
Cortex diameter:2nd hypodermal diameter	.811 ± .031
Vascular cylinder diameter:phloem fiber diameter	.824 ± .029
Vascular cylinder diameter:vessel diameter	.778 ± .036
Vascular cylinder diameter:pith cell diameter	.957 ± .008
Blade area:vessel diameter	.280 ± .080
Blade volume/petiole section:vessel diameter	.459 ± .072
Blade volume/petiole section: phloem fiber diameter	−.018 ± .091
Pith cell diameter:phloem fiber diameter	.812 ± .031
Vessel diameter:phloem fiber diameter	.575 ± .060
Petiole length:epidermal cell length	.288 ± .091
Petiole length:1st hypodermal cell length	.400 ± .084
Petiole length:2nd hypodermal cell length	.600 ± .064
Petiole length:pith cell length	.738 ± .045
Petiole length:pith cell number	.833 ± .030
Petiole shape:epidermal cell shape	.730 ± .050
Petiole shape:1st hypodermal cell shape	.483 ± .080
Petiole shape:2nd hypodermal cell shape	.535 ± .074
Petiole shape:pith cell shape	.623 ± .063
Pith cell length:pith cell diameter	.338 ± .090
2nd hypodermal cell length:2nd hypodermal cell diameter	.487 ± .079
1st hypodermal cell length:1st hypodermal cell diameter	−.039 ± .104
Epidermal cell length:epidermal cell diameter	−.341 ± .092

Volume. The correlations between cell volume and petiole volume for the four cell groups studied are presented in the first portion of the table. As was to be expected from the data on cell size, there is no correlation at all between the volume of the epidermal cells and that of the petiole. In the other cell groups, however, there is a positive correlation between these two traits which (at least in the last two) is clearly significant biometrically. Indeed, the correlation between pith cell volume and petiole volume is more than twenty times its probable error. Clearly, increase in petiole size is associated with increase in *cell number* in the epidermis and with an increase in *cell size* in the pith. A study of the regression of pith cell volume on petiole volume, however, makes it clear that the average size of the pith cells, though greater in the larger petioles, does not increase proportionally with that of the petiole as a whole, and

that increase in petiolar volume must therefore be due not only to larger cells but, in part, to more of them. An important conclusion from these facts is that the interrelationship between cell size and organ size is markedly different in different tissues.

Diameter. There is evidently no correlation at all ($+.011 \pm .091$) between the diameter of the epidermal cells and that of the petiole. In the other cell types, however, the correlation is positive and significant, and in the case of the phloem fibers and the pith cells, it is very high ($.836 \pm .027$ and $.927 \pm .016$).

It was observed that the relative size of the vascular cylinder and the cortex varied somewhat in different petioles, and the suggestion was obvious that there might be a still closer correlation between the width of these tissue systems and the diameter of their constituent cells than was the case for the entire petiolar diameter. The coefficients of correlation between cortex diameter and that of the cells of the epidermis and of the two hypodermal layers; and between vascular cylinder diameter and that of the fibers, vessels and pith cells, indicate that this is true. The epidermal correlation is still so small as to be without significance ($.190 \pm .092$), but for the other cell groups the coefficients are distinctly higher than they are with the petiole as a whole. Furthermore, a study of the regressions shows that in these cases an increase in the width of the tissue or organ is accompanied (except in the case of the vessels) by an almost exactly proportional increase in cell diameter. In other words, in the case of the pith and cortex and the fibers of the phloem, the number of cells in transverse section in all the petioles is essentially constant, and an increase in organ diameter must therefore be due almost entirely to an increase in cell diameter.

The truth of this conclusion was determined by direct observation. By dividing the diameter of the vascular cylinder by the diameter of the pith cells, the number of cells in the width of the pith can be roughly determined. The mean was approximately twenty-five cells, and the coefficient of variability a very low one, being about 12 per cent.

The diameter of the vessels is less clearly correlated with that of the petiole or the vascular cylinder than is that of any of the other non-epidermal tissues studied, and an attempt was made to determine what other factors might have a share in this result. Since previous observers have presented evidence that the rate and amount of the transpiration stream have an effect on the size of the water-conducting cells, the correlation was determined between the area of each leaf blade and the average diameter of the vessels in the petiole which supported it. This was found to be low, however, only $.280 \pm .080$. A measure of the demand

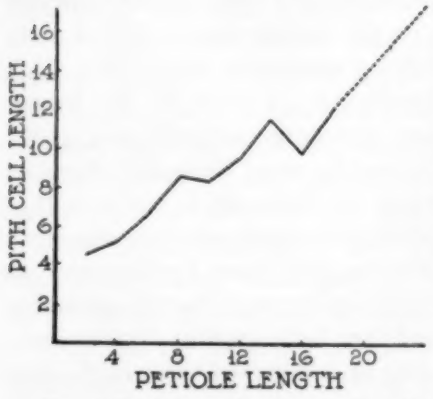
for water conduction more accurate than the area of the leaf blade is probably provided by the ratio of the total blade volume (blade area $\times$ thickness) to the cross sectional area of the petiole. The correlation between this ratio and vessel diameter was found to be $.459 \pm .072$, and thus clearly significant. It is therefore probable that vessel diameter is determined to some extent by physiological factors of this sort.

The fibers, although belonging to the vascular system, behave very differently from the vessels as far as their diameter relationships are concerned. They show a higher correlation with both petiole diameter and vascular cylinder diameter than do the vessels ($.836 \pm .027$ as compared with $.552 \pm .063$, and $.824 \pm .029$ as compared with $.778 \pm .036$), the difference being biometrically significant, at least in the former case. The ratio between blade volume and cross sectional area of the petiole (which has been shown to be related to vessel diameter) shows no correlation whatever with fiber diameter ($-.018 \pm .091$), which is thus apparently unaffected by physiological factors concerned with transport. The fibers follow much more closely the changes shown by the pith cells then they do those of the vessels, the correlation between fiber diameter and pith cell diameter being $.812 \pm .031$ and that between fiber diameter and vessel diameter only $.575 \pm .060$, the difference between these coefficients being more than three times its probable error.

Length. The correlations between cell length and petiole length, for the four classes of cells in which this could be determined, are presented in table 2. As was found to be true for diameter, the size of the coefficients increases progressively from the epidermis to the deeply seated layers of fundamental tissue. The correlation in the case of the epidermal cells is higher than any other epidermal correlation determined, but is only thrice its probable error and thus of very doubtful significance. The other three are higher and the last two (for the second hypodermal layer and the pith) are undoubtedly significant biometrically. Increase in petiole length is clearly associated with increase in cell length in cortical and pith tissues. A study of the regressions, however, shows that the two increases are not proportional, but that cell length, though much greater in the longer petioles, does not increase proportionally with petiole length, so that the longer petioles not only have longer cells but must have more of them.

This conclusion was confirmed by direct observation. The number of pith cells in the length of the petiole was determined by dividing the average pith cell length into the petiole length. Pith cell number was then correlated with petiole length and a positive coefficient of $.833 \pm .030$ determined. Regression seems to be linear, but it evidently cannot be so

both here and in the case of pith cell length and petiole length, since petiole length is the product of these two factors. Presumably regression in neither case is truly linear, though it is sensibly so, and the correlation coefficient is thus not a strictly accurate measure of the relationship. The essential point, however, is that an increase in petiole length involves an increase both in the length and in the number of pith (and cortical) cells. This relationship is shown in figures 4 and 5, where length and number of pith cells are plotted against petiole length.



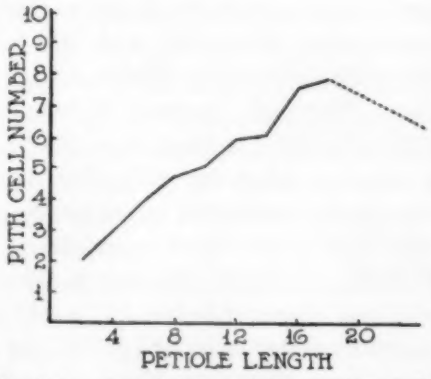


Fig. 4 (left). Graph showing the relation between petiole length (in centimeters) and pith cell length (in .01-mm. units).

Fig. 5. (right). Graph showing the relation between petiole length (in centimeters) and numbers of pith cells (in units of 100) in the length of the petiole.

The number of pith cells in petiole length varies much more than in petiole width, the coefficient of variability of the former being 43.5 per cent and of the latter 12.0 per cent. Evidently cell division in the longitudinal direction persists much longer than in the transverse.

Shape. On the basis of the figures presented above it is to be expected that there should be positive correlations between the shape index of the petiole and those of its constituent cells, and the coefficients presented in table 2 indicate that this is true. It should be emphasized here that, as in some of the previous correlations, the variation in the two traits is far from proportional. Shape index in the cell is much less variable than in the petiole. A unitary change in the index of the epidermal cells, for example, is associated with one about ten times as great in the petiole. Nevertheless, for all the tissues there is an undoubtedly significant correlation between cell shape and petiole shape. That the morphogenetic implications of this fact are perhaps not as great as the size of the coefficients would imply is indicated by the fact that the correlation is actually

highest for the epidermal cells, which in all other respects show little or no relation to petiolar characters. These correlations would readily be produced if (as seems probable) increase in petiole length persisted for a time after cell division in length and petiolar growth in diameter had slowed down or ceased.

DISCUSSION

There are a number of points at which the facts brought out by the present study seem to bear on the problem of the interrelation of cell and organ traits.

The great diversity between cells of different tissues as to their variability and as to their relations to the size and shape characters of the petiole make clear the impossibility of deriving from the study of any single tissue (like the epidermis) conclusions which are of general applicability. An explanation for these marked differences between tissues is difficult to determine. The most plausible suggestion, perhaps, is that constancy in cell size (and possibly shape) is associated with a relatively high degree of functional activity and physiological specialization, and variability with a relatively inactive and generalized condition. In the leaf blades borne by the petioles studied, cell size in the upper epidermis and the palisade layer was measured and found to be essentially constant in leaves of very widely diverse areas. The vein islets, or patches of mesophyll tissue between the ultimate ramifications of the veins, were also of constant area. Practically no differences in cell characters could be observed in leaf blades which varied widely in their own dimensions. These results agree with those of practically all other investigators who have studied leaf blade tissues. Both the epidermal and mesophyll cells remain alive until the death of the organ, are rich in protoplasm and active metabolically, and apparently are rather highly specialized. It is quite understandable that in cells of this sort there is for each tissue an optimum surface-volume relation which cannot well be exceeded, and that during growth cell division takes place at a rate which will insure the fairly constant maintenance of this size. On the other hand, in the unspecialized fundamental tissues, particularly the pith, there is little functional activity and many of the cells (at least in *Acer*) die soon after growth is finished. The physiological importance of great constancy in cell size and shape in such tissues is by no means obvious. Intermediate conditions might be expected to obtain in the outer layers of the cortex, however (as was actually found to be the case), for here many of the cells possess chlorophyll and are doubtless progressively more specialized and more active; and they are found to become more uniform in size

until in the epidermis essential constancy is attained. It should be noted in this connection that marked differences in plasticity between tissues have also been observed by other investigators. Küster (1925), for example, calls attention to the fact that in general the epidermis will rarely proliferate or take part in the formation of callus, whereas the pith will readily do so, its cells often becoming strikingly different from their normal size and shape. These facts are in precise agreement with the results of the present study.

The various tissues differ not only in cell size but in the persistence and direction of cell division within them. Comparatively little in this field is known from direct histological observation, but an analysis of mature tissues such as has here been made enables us to recognize certain important facts. A study of transverse sections of the very short petiole present in leaf primordia in winter buds shows that most of the pith cells and a large proportion of the cortical cells are already present, at least in the basal leaves. Later growth of the petiole in the transverse direction is accompanied by comparatively little cell division in these tissues, but is due chiefly to the expansion of cells which are formed very early. In the upper leaf pairs there is a considerable increase in cell number transversely when the bud begins to open, but the close correlation between petiole diameter and the diameter of its constituent fundamental tissue cells, together with the data for the regression of these on each other, indicate that cell division in the transverse direction ceases relatively early in all cases. There is a marked increase in cell number in the vascular bundles during the development of the petiole from its primordium in the bud and, as has been pointed out, various physiological factors doubtless influence to some extent the diameter of the vessel cells; but the relatively high correlations between petiole diameter and those of fibers and vessels show that in these tissues cell division in the transverse direction must cease relatively early. In other words, for the tissues inside the epidermis the number of cells in the transverse direction (and thus the frequency of longitudinal cell divisions) is relatively constant, and the bulk of petiolar growth in diameter depends on the extent to which these cells enlarge transversely after cell division has ceased. Organ size in this dimension is closely paralleled by cell size, and an increase in the former is accompanied by a proportional increase in the latter. In the epidermis, however, an entirely different condition obtains, for here cell diameter is essentially constant and is quite unrelated to differences in the diameter of the petiole, indicating that the longitudinal divisions which increase the number of cells in the epidermal layer persist for a much longer time than do similar divisions in the underlying tissues,

and are proportional in number to the size attained by the organ as a whole. Here an increase in organ size is accompanied by more rather than larger cells.

The same contrast between epidermal and fundamental tissues is also evident in longitudinal growth, but it is not quite so sharp here, for the elongation of the petiole from leaf primordium to maturity is accompanied by meristematic activity throughout the organ. Long petioles always have more cells than do short ones, so that much of the growth in length (in contrast to the growth in diameter) must be due to an increase in actual cell number. The relation between cell division and growth is markedly different in different tissues, however. In the epidermis the number of cells is proportional to the length of the petiole, indicating that cell division must persist here until petiolar growth in length has nearly or quite ceased. In the pith, on the contrary, although growth in length is accompanied by cell division, a very considerable portion of such growth is due to cell elongation, as is proved by the marked correlation between pith cell length and petiole length. This must mean that, in this tissue, transverse cell divisions fail to keep pace with the lengthwise growth of the organ as a whole and that the later increments of growth in length are accompanied by cell elongation, rather than by such a persistent cell division as is found in the epidermis. As to whether division takes place in progressively larger cells and at a progressively slower rate, or whether it is maintained actively up to a certain point in the young growing tissue and then ceases (later growth being entirely due to cell elongation), is not definitely known in this case. In Lehmann's careful analysis (1926) of growth in potato tubers the former condition was found to obtain, the early increments of growth being due chiefly to increase in cell number and the later ones chiefly to increase in cell size. The fact that the longest petioles here studied have pith cells five times as long as the shortest ones suggests that in this tissue cell division probably ceases relatively early.

In the outer cell layers of the fundamental tissue there is a progressive decrease in the correlation between cell length and petiole length, the coefficients being, for pith cells $.738 \pm .045$; for the next to the outermost cell layer of the cortex, $.600 \pm .064$; for the outermost layer, $.400 \pm .084$, and for the epidermis, $.288 \pm .091$. It should be noted that these relations are not affected by the actual length of the cells, for in the second hypodermal layer the average cell length is essentially as great as in the pith but the correlation with petiole length is significantly less. In other words, in cell layers intermediate between typical fundamental tissue and epidermis, cell division in the transverse plane persists to a relatively later and later stage until in the epidermis its frequency is directly pro-

portional to the amount of growth. This series parallels exactly the one for variability in cell size, in which the cells of the pith were at one extreme and those of the epidermis at the other; and a similar suggestion as to the reason for this series may be made in the present case. Position on the shoot may also play some part here, since it was found that in progressing from the basal leaf pair to successively higher ones, the pith cells, though shorter in actual dimensions, became *relatively* longer in proportion to petiole length, thus indicating that cell division ceases first in the terminal petioles and last in the most basal ones. There is evidently need for much more thorough study of the actual process of growth in tissues of this sort.

The picture thus presented of the relation between the characteristics of the petiole and the size and shape of its constituent cells emphasizes the complexity of the whole problem. The data are by no means conclusive for a solution of the question as to whether the size and dimensional relationships attained by the petiole are simply a summation of these traits in its constituent and quasi-independent cellular units; or whether the observed petiolar characters are determined by factors acting on the whole mass of tissue regardless of how minutely it is divided into cells. If conditions obtaining in the epidermis, where all the cells are essentially of the same size and shape, held true throughout the petiole the facts could easily be construed to support the former hypothesis, or at least would not be inconsistent with it. Conditions in the fundamental tissue, however, which constitutes by far the largest portion of the volume of the petiole, are so different from this as to suggest that the second hypothesis may explain the facts more simply. In this tissue, and particularly in its larger portion, the pith, the cells are not only variable in size in a given organ but even the average volume per petiole is so diverse that in some petioles it may be nearly eighty times as great as in others. In shape, too, there is much greater variability in the pith than in the epidermis, largely because the pronounced variability in the length-width ratio of the petiole is reflected in the dimensional ratio of its pith cells.

The conception of the petiole as an aggregation of units fundamentally similar in size and shape, which by their interaction produce the characteristics of the organ as a whole, meets with further difficulties when we examine the dimensional relationships of the cells themselves. If these cells are essentially similar individual entities, they might be expected to have a relatively constant shape, at least in such a homogeneous tissue as the pith. We have already seen that the variability of cell shape in this tissue, as measured by the coefficient of variation of its shape

indices, is rather high. Another measure of the uniformity of cell shape is the correlation which exists between cell length and width. If a cell is relatively constant in shape, whatever its size, this correlation should be high, and vice versa. In the pith cells, the correlation of average cell length with average cell width, however, is only $.338 \pm .090$, and is thus low and of doubtful significance. It is instructive to compare this figure with the correlation coefficient between pith cell width and petiole width ($.927 \pm .016$); and with that between pith cell length and petiole length ($.738 \pm .045$). Evidently the width of a pith cell is far more closely related to the width of the petiole of which it is a part than it is to the length of that cell; and the length of the cell is more closely related to the length of the petiole than it is to the width of that cell. The differences are so marked as to be of undoubted biometrical significance, being about 6.5 times the probable error in the former case and 4.0 times in the latter. In the other cell groups similar results appear, in two cases the correlation even being negative in sign. These facts certainly suggest that the cellular unit has little in the way of a fixed and specific individual shape, but that its dimensions may be determined not by intracellular factors but rather by the relative amount of growth in various dimensions which is attained by the organ of which the cell forms a part. Of course, any organ is the sum of its component cells and in that sense may be said to owe its characters to their combined effect; but the problem which we are discussing goes much deeper than that and inquires whether the ultimate unit involved in the process of development is the individual cell, which by its multiplication builds up a quasi-colonial organic entity, or whether the unit is a mass of tissue, an organ or even the entire organism. No decisive evidence is at hand to determine definitely for us which of these two alternatives is correct, but at least in the fundamental tissue of the maple petiole here described there seems to be so little constancy in either the size or the shape of the cells that it is very difficult to regard them as specific morphogenetic units.

If we take this attitude and regard as the unit in development an entire cellular mass (in this case perhaps the petiole as a whole) is it possible to explain the facts more simply? The assumption of some necessarily vague factor for the "organ as a whole" is certainly not helpful. It is quite possible, however, to conceive of perfectly definite factors in the external or internal environment of an entire mass of tissue which might profoundly change its size and shape irrespective of the particular extent to which the tissue mass was subdivided into cells. Modifications in the permeability of the protoplasmic membranes, changes in the osmotic concentration of the sap, secretion of various substances

(hormones or others) which so affect the cellulose wall as to make possible its greater extensibility, and other changes which are either directly effective on the protoplasmic mass as a whole or are readily diffused throughout its extent, have been called upon to account for size changes in plant tissues and are not necessarily accompanied by increase in cell number. It is quite conceivable that changes of this sort, initiated by environmental factors such as light and gravity, may operate to modify very markedly the size to which a plant organ may grow. In the horizontal shoots of *Acer*, for example, the leaves are anisophyllous, the lower member of each vertically oriented leaf pair having a much longer and stouter petiole than the upper one. Whether this is due, as earlier writers and the author (1923) suggest, to the effect of gravity; or whether, as others believe, light is the agency chiefly concerned, it is evident that some environmental factor, acting upon the entire organ, has induced these marked differences. Increase in size in certain tissues has been attained chiefly by cell enlargement and in others chiefly or entirely by increase in cell number, but it seems to be the protoplasmic mass as a whole (with its non-living accretions), variously subdivided into smaller units, which is the developing entity.

The division of living substance into relatively small units (the cells) has so many obvious advantages that one can readily understand its almost universal occurrence among other than very minute organisms. Indeed, differentiation and the complex physiological activities of the higher plants and animals would otherwise be quite impossible. If the cell habit is the result of a subdivision of living substance for *physiological* reasons, this subdivision will evidently be more precise and uniform in tissues of high physiological specialization, like the epidermis, than in relatively unspecialized tissues like the pith, with resulting differences in variability in cell size; but if the cell is a *morphological* unit by the aggregation of which the organism is built up, its size, though of course differing from tissue to tissue as the result of histological differentiation, should not be more variable in one homogeneous tissue than in another. The fact that in the material here studied a marked difference of this kind has been found to exist evidently favors the former hypothesis. In the cells of the central portion of the pith, which die almost as soon as they are produced and which are of no apparent functional importance, physiological complications seem to be eliminated and the purely morphogenetic aspect of our problem can be studied more directly. The evidence here presented at least emphasizes the importance of approaching the problem of cell size by means of a complete histological analysis rather than through the study of a single tissue; and the necessity of distinguish-

ing the purely physiological factors in the problem from those which are more directly concerned with growth and morphogenesis.

SUMMARY

In a series of sixty leaves from a tree of *Acer saccharum* measurements were made of the various dimensions of blade and petiole, and the volumes of both computed.

For the epidermis, the first and second hypodermal layers of the cortex, the phloem fibers, the vessels, and the pith, the average diameter and cross sectional area of the component cells was determined in each petiole; and in all these tissues except the fibers and vessels the average cell length, volume, and shape index per petiole were also determined.

In all traits the pith cells were found to be much more variable than those of the epidermis, with the other tissues intermediate.

Between the diameter, length, and volume of the petiole and the diameter, length, and volume of its constituent epidermal cells no correlation was found; but between the petiole and the pith cells, for these traits, correlation is high. Intensity of correlation is intermediate in the intervening cell layers.

In the fundamental tissues, which constitute the bulk of the petiole, the number of cells in transverse section is essentially constant, so that differences in petiole diameter are closely associated with differences in cell size rather than in cell number; but in longitudinal sections both number and length of cells increase with petiole length. In the epidermis, differences in organ size are associated entirely with differences in cell number. These facts suggest that cell division persists longer in certain tissues, and in certain directions, than in others.

Vessel diameter is related in part to demand for water conduction as measured by the ratio between blade volume and cross sectional area of petiole.

In all tissues cell shape seems to be correlated to some extent with petiole shape.

The marked differences between tissues in the variability and the petiolar correlations shown by their cells makes it evident that general conclusions as to the relationship between cell traits and organ traits cannot be drawn from a study of any one tissue.

It is suggested that this variability in cell behavior may be due to differences in degree of physiological specialization, highly specialized tissues having relatively constant cell characters and unspecialized tissues relatively variable ones.

The evidence here presented is somewhat difficult to reconcile with

the conception that an organ is an aggregation of quasi-independent cellular units, specific in character, which by their interaction determine the traits developed by the organ; but rather favors the view that those factors which determine the form and size of an organ affect the entire mass of its living substance, regardless of how extensively this may be subdivided, for physiological efficiency, into individual cells.

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Pollen grains in the identification and classification of plants
V. Haplopappus and other Astereae: the origin of the furrow configurations

ROGER P. WODEHOUSE

(WITH PLATE 1 AND FOURTEEN TEXT FIGURES)

The present series of investigations has as its aim the analysis of pollen-grain forms in the different tribes of the Compositae, to discover their origin, their phylogenetic distribution, and their evolutionary trends.

Some of the characters of pollen grains are unquestionably phylogenetic: that is to say they are constant within the species, and have a distribution among the different species similar to that of the grosser anatomical characters by which the plants are classified; they appear in the same associations and with little modification in closely related species, and in different associations, and in variously modified forms in distantly related or unrelated species. For example, one of the most outstanding characters of the pollen grains of the Compositae is the possession of spines of greater or less prominence associated with furrows (generally three) of a particular character. The spines exhibit various modifications in shape, size, and distribution over the surface of the grain, in the different branches of the family. In some groups they are long and sharp; in some they are short and rounded; in others they are greatly reduced, entirely absent, or represented only by vestiges. But always they are practically the same in all the grains of all the individuals of any species, and diverge but little in the grains of closely related species. Such cell characters I have designated as *emphytic* (Wodehouse, 1929). They are the outward expression of specifically inherited cell tendencies.

Some of the characters of pollen grains are apparently much less phylogenetic, being distributed at random without regard to phyletic relationships; and it frequently happens that these are the more conspicuous features of the grains. For example the possession of three furrows is generally the most conspicuous character of the pollen grains of the Compositae. Nevertheless a diligent search of the pollen of almost any species of this family will reveal at least some grains with four, six, or other numbers of furrows. Furthermore the pollen of some few species of Compositae never exhibits grains with three furrows; for example those of the dahlias have invariably six, though this plant's nearest relatives, the sunflowers, *Cos-*

mos, *Silphium*, and other members of its subtribe, the Heliantheae, have predominantly three furrows. Still other species exhibit grains with furrows ranging in numbers from two up to twelve. The number and arrangement of the furrows are imposed upon or acquired by the grain during its formative period, and their variations are in some cases the result of the various arrangements of the cells in the tetrad. Characters originating in this fashion I have designated as *haptotypic* (Wodehouse, 1929). They are of relatively little use in the identification or classification of pollen grains. Hence the necessity of clearly distinguishing whether characters are emphytic or haptotypic.

Two years ago appeared a *Phylogenetic Study of the Compositae* of revolutionary import (Hall, 1928). In this work the author assembles under the single generic name, *Haplopappus*, plants of the Astereae which in recent taxonomic work had been regarded as belonging to twenty or more genera; and he reduces many well known species to the rank of varieties, minor variations, or even to synonymy, indicating that these plants represent a compact and much more closely related group than was formerly supposed. In this new arrangement, however, the former generic assemblages are retained for the most part as sections of the genus; and, what is of greater interest, their relative position in the evolutionary scale and their degrees of relationship to each other are clearly indicated.

These phylogenies are carried out to their ultimate ramifications through the species, subspecies, and varieties,—an arrangement which aims to give a comprehensive view of the exact interrelationships within the entire group, comprising some 150 species together with many subspecies and variations. For this reason the genus *Haplopappus* was chosen for this study in the endeavor to discover the phylogenetic behavior of pollen-grain characters in the tribe Astereae.

The results of the present communication are based on the study of the pollen grains of 48 species and varieties of *Haplopappus*, covering all of the North American sections and three of the South American sections of the genus as constituted by Hall. As a basis of comparison, an examination was also made of the pollen of 23 other species in 17 genera of Astereae. Of those exhibiting irregular or unusual forms, pollen from all available specimens was examined, covering sometimes as many as five different collections; otherwise pollen from a single specimen was deemed sufficient to represent each species.

In all cases measurements were made of the diameters of the grains, and the length and distance apart of the spines. The texture of the exine and the characters of the furrows were also observed, and a record kept of atypical forms, such as giants, dwarfs, and grains with atypical numbers

of furrows. The record of atypical forms is shown in table 1, but all others have been omitted, as their monotony would unnecessarily burden the text.

The pollen grains of *Haplopappus* (plate 1, fig. 10) are spherical or slightly flattened. In size the normal grains range from 19.4 to 35.3 microns, averaging about 28.5 microns, just a little larger than those of the other Astereae, which, in the species examined, range from 16.5 to 31.9 microns, averaging about 22.8 microns. The grains are always provided with well developed spines, which, in their form, and the appearance which they present of uniformity in size, shape, and distribution over the surface, are characteristic for the grains of the Astereae. This type of spine is short, broad at the base, and nearly conical in shape. There is some variation in the different species in the amount of tapering of the spines: sometimes they end abruptly, as the top of a pyramid, and sometimes they taper slightly into a more or less acuminate tip. Though the shape of the spines is occasionally obviously slightly different in the different species, a comparison of several hundred measurements, covering all species examined, shows that this variation is too slight and intangible to lend itself to analysis. The length of the spines and their distance apart are likewise somewhat various in the different species, but these characters are also too slight to be of value in discriminating species within the genus, though there is some evidence that the differences in spine length are sufficiently pronounced to distinguish some of the other genera of the Astereae. The measurements of the lengths of the spines within the genus *Haplopappus* often vary as much as 25 per cent: but I question whether such measurements are a closer expression of facts, on account of the inherent difficulties of making them.

The arrangement of the spines in the grains of *Haplopappus* is highly uniform and regular, patterned after the arrangement assumed by spherical bodies of uniform size when crowded together—as, for example, when shot are caused to pack closely in a single layer on a plain surface. This arrangement may be described by saying that if any one of the shot be regarded as a center it will be surrounded by six others, all in contact with it and with each other. In other words the centers of the spheres are all equidistant from each other along the sides of an equilateral hexagon, and equidistant from that of the sphere at the center of the hexagon. In the distribution of the spines over the surface of the grains such an arrangement appears to be as faithfully followed as is structurally possible. But the hexagonal pattern is modified by the furrows, the spines showing a tendency to line up along their margins. Thus we find, upon measuring the angles and intervals between the spines, even in the most regular hexagonal configurations, that differences amounting to more than 30 per cent

are encountered in their distance apart, and the internal angles of the hexagons are not always equal. Frequently, particularly in the smaller grains, pentagonal configurations are interspersed among the hexagonal.

The distance apart of the spines can be measured with a fair degree of accuracy; yet such measurements show a surprising variation. Hexagonal groups of seven in grains offering favorable conditions for such observations were measured; in a giant grain of *H. acaulis glabratus* (D. C. Eaton) Hall the twelve measurements taken in all directions between the seven spines of a single hexagonal group, were 3.7, 4.6, 4.6, 4.6, 4.6, 3.4, 4.6, 4.3, 4.7, 4.0, 4.0, 4.0 microns. The grain upon which these measurements were made was 34 microns in diameter—large enough so that its spherical curvature could not seriously affect the measurements over so relatively small an area as that occupied by a single hexagonal group of spines; yet we note a variation in the distance between them ranging from 3.7 to 4.7 microns, or more than 25 per cent; and when measurements between pairs of spines more widely separated are compared, the range of variation runs still higher. Throughout the entire genus the average of this distance for each species varies from 3.2 microns in *H. divaricatus* (Nutt.) Gray to 7.1 microns in *H. propinquus* Blake. In fact the distance apart of the spines in the grains of all except three species lies between 4.3 and 5.9 microns, with the majority very close to 5.1 microns.

The texture of the exine of all species of *Haplopappus* is granular: the roughening is rather faint between the spines, but at the bases of the spines it becomes a little coarser and somewhat more sharply defined, though not extending far up the shafts of the spines, which are quite smooth and homogeneous in appearance.

With few exceptions it is difficult or impossible to distinguish the grains of the other genera of the Astereae from those of *Haplopappus*. Among the exceptions are the members of the subtribe Grangeineae. The grains of this group offer only the distinction, of doubtful value, of their smaller size, which ranges, in the five species examined, from 17.7×16 to 21.6×20 microns; yet their spine length is almost uniformly 2.3 microns, which is approximately the same as that of the much larger grains of *Haplopappus*. The small size of the grains of the Grangeineae, together with their relatively large spines, gives them an appearance strikingly different from that of the grains of the other Astereae. This size character is also shared by the grains of *Microglossa volubilis* DC. and *M. sessilifolia* DC. of the subtribe Conyzeae, but not by the other members of that subtribe, for the grains of *Haastia* and *Psiada* of the same subtribe are essentially the same as those of *Haplopappus*. This character is, however, found again in the grains of *Boltonia* of the subtribe Heterochromeae. Taken altogether

these differences are scarcely marked enough to serve as reliable guides to relationship: they are fortuitous in distribution and not associated with any other visible characters. All that is even suggested by the pollen-grain forms of the Astereae is that the members of the subtribe Grangeineae, having slightly but consistently smaller grains, stand apart from the others. All the other species of which I have examined the pollen might, as far as their pollen-grain forms are concerned, quite well be included in the genus *Haplopappus*.

The pollen of most species of *Haplopappus* presents, perhaps, more than the usual number of abortive grains. Among these, in about one half of the species and distributed at random, were observed a number of dwarf grains (fig. 6) which are apparently empty, obviously sterile, and only a very small fraction of the normal size. Such grains have been observed in the pollen of other groups by many investigators and explanations advanced for their origin. But these do not concern us at the present time. Suffice it to say that it is well known that if a pollen grain aborts after the first rudiments of the exine are laid down its development is carried to completion in all its details, though the cell itself be entirely empty, and thus it is that the external characters of the dwarf grains, though dead and empty, are comparable with those of normal and healthy grains.

A comparison of the dwarf, normal, and giant grains (table 1) shows that the length of the spines and their distance apart bear no relation to the size of the grain; the dwarfs do not, as a consequence of their small size, have spines reduced or packed any closer together, and the giants do not have giant spines, nor are they more widely separated. It is as though each grain had it its disposal a quantity of exine of a standardized pattern; and of this it appropriates enough to cover its surface, which is accomplished by a little stretching here and there to fit the curvation or a little compressing to fit awkward corners, but uses it without otherwise modifying the standardized pattern, whether the grain be a dwarf with only a small surface area or a giant with several times the surface of normal grains. The total number of spines on these grains therefore is purely a function of their surface area, and this is inconstant in normal healthy grains. The number of spines per unit area, however, or spine-frequency, is a definite and useful character. The spine-frequency, spine-length, and the various other characters of the exine are emphytic.

The basic morphogenetic principle involved is that the size of the pattern elements and the size of the grains are not positively correlated. I shall discuss elsewhere the question as to the relation of these facts to the non-correlation of cell size and organ size, as described by Amelung and now generally accepted.

Throughout the entire genus *Haplopappus* there is little variation in the emphytic characters, which is entirely in keeping with the close relationship believed to exist between all these species: and but little more difference is seen between those of *Haplopappus* and most of the other Astereae. We are forced to the conclusion that the interrelationships of these species are so close that their differences do not come to visible expression in basic characters such as those of the structure of the pollen grains. On the other hand, the haptotypic characters show an enormous variation not only among different species, but among different individuals of the same species, and even among different grains from the same plant.

HAPTOTYPIC CHARACTERS

The basic or typical form of the pollen grains of *Haplopappus* (fig. 10) and other species of Astereae is similar to that of the grains of most Compositae. They are spherical or oblate spheroidal. The walls are thick and immobile, and as noted, are provided with the so-called 'germinal furrows'; these are generally three, equally spaced around the equator, which they cross at right angles; they converge along meridional lines towards two centers which, it follows, are triradiate and at opposite poles of the sphere. The axes of the furrows, if extended, would thus intersect at angles of one third of a circle or 120° at each of the poles, and thus divide the surface of the spheroid into three equal lunes. Though there is some variation in the lengths of the furrows, among the different species, they never quite meet, always ending some distance short of the centers of convergence. Such a form of grain is called tricolpate (*τρίς*, three and *κόλπος*, furrow).

The furrows appear as deep gashes cut into the exine. When the grain is moist they spread widely open; and are seen to be crossed by a thin layer of the exine, which, in this region, lacks the granular texture and characteristic sculpturing of the general exine. In the center of each is a rounded aperture or pore through which the pollen tube may grow at the time of germination, and through which the germinal papilla always bulges when the grain is moist and expanded. The exine crossing the furrow is elastic, and permits the opening and closing of the furrow, thus accomodating changes in volume of the grain with the absorption and liberation of moisture. In the pollen of many species are found a varying proportion of grains with more or fewer than three furrows. Sometimes these present great irregularity and asymmetry in arrangement and form, but more often they are highly symmetrical, the various numbers of furrows forming different patterns in the expression of their symmetry arrangements. These configurations are well defined, and with some study, it is generally possible to assign any of the grains with supernumerary furrows to one or another of a rather small number of different type arrangements.

The distribution of these configurations among the different species is quite fortuitous, the various forms occurring abundantly in the pollen of some specimens and being entirely absent from that of others of the same species. The most usual atypical numbers of furrows are six and four. Other numbers of furrows encountered less frequently are twelve, nine, and very rarely two, and eight, and in one specimen, none at all.

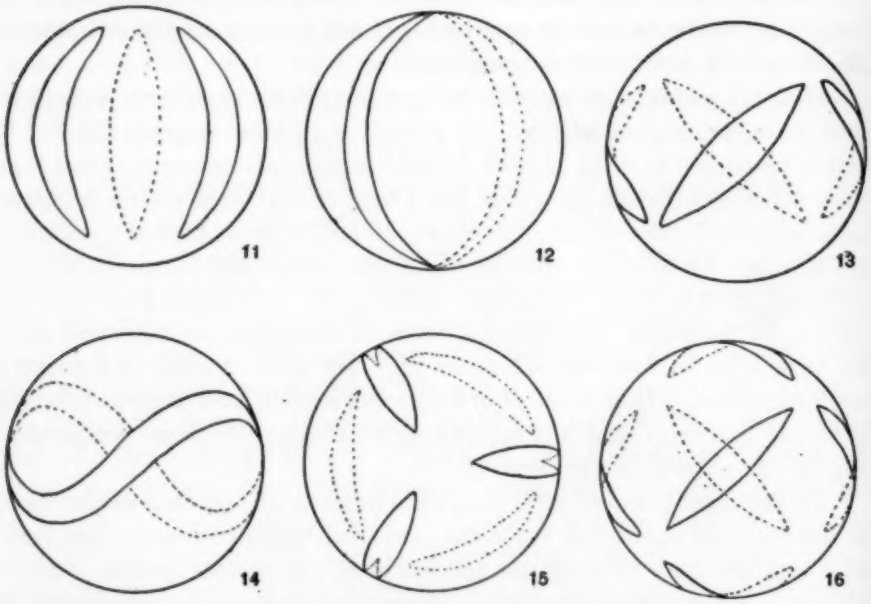
On account of the relations that the configurations of the atypical numbers of furrows bear to each other it will be best to discuss them in the ascending order of their complexity.

Acolpate grains. Grains with no obvious furrows have three apertures and pores, and appear healthy, and normal in all other respects (fig. 8). It might be argued that the furrows, instead of being absent, are so short that they coincide with the apertures, but I believe that such a view is untenable because the apertures are quite round and without hint of meridional orientation. Only in one specimen of *Haplopappus* was the acolpate form observed, and that was *H. acaulis glabratus* (D. C. Eaton) Hall (*Gooding 1111*). In the pollen from this specimen all the grains are alike and show no suggestion of furrows; otherwise they are quite normal and notably uniform, differing from those of other species only in their somewhat larger germinal apertures, which is apparently an adaptive response compensating for the absence of the furrows.

At first sight it would seem that this character should be regarded as of at least specific value, and not in the present category; but an examination of the pollen from all available specimens of this species reveals the fact that it is not a specific character. The pollen grains of two specimens of *H. acaulis glabratus* (*Nelson and McBride 2173, Nelson and McBride 1914*) and one of *H. acaulis typicus* Hall (*Baker 987*) (see table 1) do not possess this character; instead their grains have the well developed furrows typical of the genus. There can be no question of the identification of the specimens, for they are cited by Hall (1928). Furthermore the identifications of these specimens were kindly confirmed for me by Dr. Rydberg and Dr. Gleason of the New York Botanical Garden. Consequently I feel justified on *a priori* grounds, in regarding this character as haptotypic. The presence of three well developed apertures without furrows suggests that the conditions which produce the furrows are not identical in character with those which produce the apertures, and in this particular instance are lacking or deficient.

Germ pores and furrows are not necessarily associated. Pores without furrows are rare in the pollen grains of the Compositae. I have observed this character as an abnormality in only one other instance, an unidentified specimen of *Baccharis,* but it is characteristic of the grains of *Car-*

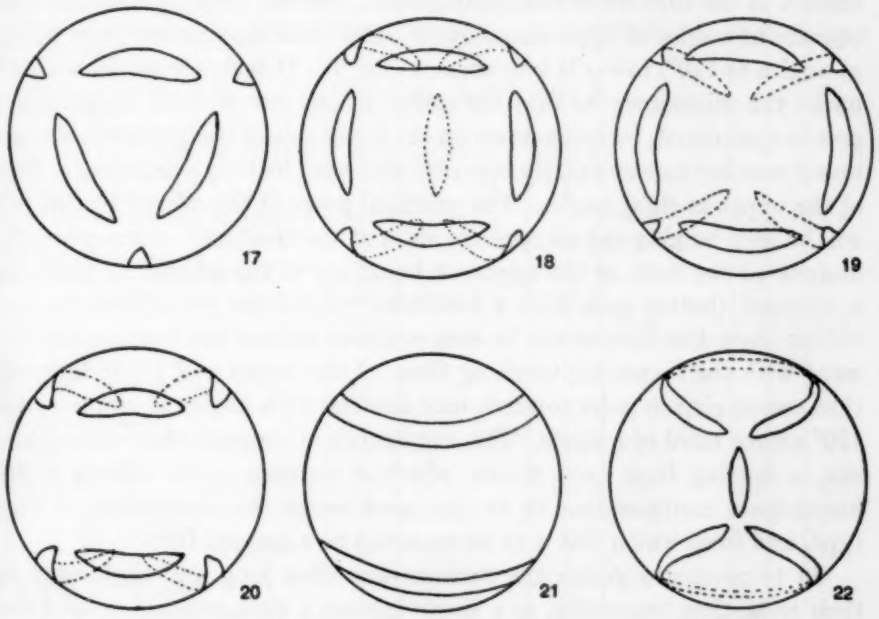
thamnus lanatus L. and *Centaurea melitensis* L. Nevertheless it is common in other groups as, for example, the Betulaceae, several species of *Calandrinia* (Portulacaceae), and many others. On the other hand furrows without apertures are common in the grains of the Compositae, as we shall see in those with supernumerary furrows, for such grains seldom have more than six apertures, though they may have as many as twelve furrows.



Figs. 11–16. Diagrams of furrow arrangements. 11. Tricolpate: three furrows equally spaced and converging towards two centers. 12. Dicolpate, with the two furrows opposite and united. 13. Tetracolpate: four furrows converging in pairs towards four centers; cf. hexacolpate. 14. Zigzag form, probably derived from the tetracolpate by the fusion of the furrows at their converging ends. 15. Hexacolpate, six furrows converging towards four centers, one above and three below the limb or median optical plane. 16. Hexacolpate, viewed with one furrow uppermost; focusing down brings into view another furrow exactly opposite, but with its long axis crossing that of the upper at right angles, while the other four furrows may be seen curving down over the limb.

Dicolpate grains. When the grains have only two furrows they are generally in the triradiate position of those of normal tricolpate grains (text fig. 11), with their axes converging towards the two centers at angles of 120°, as if one of the normal three had been dropped without otherwise disturbing the organization of the grain. When in this arrangement the furrows have a tendency to be extended and become fused at one or both centers of convergence, as if the absence of the third furrow led to the

lengthening and fusion of the remaining two. This type of grain would be represented by dropping out from figure 11 the furrow shown in dotted line as on the under side of the grain. Occasionally a careful inspection of dicolpate grains with furrows in this position reveals a trace of the third furrow, without its aperature, represented by a slight rift in the exine, suggesting that this form arises merely by the partial or complete suppression



Figs. 17–22. 17. Nonacolpate: nine furrows converging towards six centers; viewed with one of the spherical triangles uppermost. 18. Nonacolpate, viewed with one of the spherical squares uppermost. 19. Octacolpate: eight furrows in the same configuration as the nonacolpate, except that one is missing. 20. Hexacolpate: derived form, six furrows in the same configuration as the nonacolpate, except that the three which formed the meridional sides of the spherical squares are missing. 21. Zonate. 22. Half zonate. Both this and the zonate form are apparently derivatives of the nonacolpate type.

of one of the furrows. In another arrangement of furrows in dicolpate grains they are exactly opposite each other. When so arranged they nearly always coalesce at both ends and completely encircle the grain as a single furrow (fig. 12), but with two germinal pores opposite each other (fig. 7).

Dicolpate grains of both forms constitute about one quarter of the grains of the pollen of one specimen of *H. lanuguinosus typicus* Hall (*Cusick 3282*). With furrows in the triradiate position they have been found in *H. spinulosus glaberrimus* (Rydb.) Hall and *H. spinulosus scabrellus*

(Greene) Hall; with furrows opposite in *H. ciliatus* (Nutt.) DC. Outside of this group they have been found in the pollen of *Hecastocleis Shockleyi* Gray among the Mutisieae.

Tetracolpate grains. When the grains have four furrows they are equally spaced on the equator (fig. 13), but the axes of such furrows never cross the equator at right angles and converge towards the poles, after the fashion of the furrows of tricolpate grains. Instead they always cross the equator at angles of approximately 45°, and their axes converge in pairs, at angles of 120°, towards four centers (fig. 9). If such a grain is oriented under the microscope so that the center of one furrow with its germinal pore is uppermost, focusing down on the lower side of the grain will always reveal another furrow exactly opposite, but with its long axis crossing that of the upper at right angles. The germinal pores of the other two furrows will be seen bulging out on opposite sides of the 'horizon'—more properly designated the limb, or the apparent boundary of the sphere. As the focus is changed (better seen with a binocular microscope giving stereoscopic vision) these two furows will be seen to curve around the horizon and inward with their axes approaching those of the upper and lower furrows, thus converging in pairs towards four centers, with angles of convergence 120° or one third of a circle. This configuration suggests that a third furrow is missing from each center, which if restored would complete the hexacolpate configuration to be discussed under the description of that type, and from which this may be regarded as a derived form.

In tetracolpate grains the furrows are often long and coalescent at their ends, thus traversing, as a single furrow, a zigzag course around the grain, intersecting its equator four times at angles of 45°. From such furrows any one or more of the germ pores may be absent and the angles of convergence may be lost in broad sweeping curves causing the furrow to assume much the form of the curved seam in the fabric covering of a tennis ball (fig. 14).

The tetracolpate form, with furrows converging towards four centers, has been found, among the grains of *Haplopappus* and the Astereae, in eleven specimens from nine species. In *H. lanuginosus typicus*, it is abundant in the Cusick specimen, rare in the Howell specimen, and absent from the Kelsey and Leiberg specimens (cited in table 1). It is present in both the fused and unfused forms in *H. lanuginosus Andersonii*. In *H. MacLeanii* it is present in both the Tarleton and Gorman specimens (table 1). It is also occasionally encountered in most of the other groups of the Compositae, and constitutes about one half of the grains of *Ambrosia psilostachya* DC. and *A. coronopifolia* T. & G. Outside of the Com-

TABLE 1

Comparison of normal, dwarf, and giant pollen grains from seven sections of Haplopappus and two other genera of Astereae, showing dimensions, length of spines (Sp.), and spacing of spines (Dis)

	NORMAL			DWARF			GIANT			NOS. OF FURROWS
	Diam. in μ	Dis.	Sp.	Diam. in μ	Dis.	Sp.	Diam. in μ	Dis.	Sp.	
§BLEPHARODON										
H. spinulosus glaberrimus (*Tweedy 3045*).	25.1	5.3	1.1				29.6	4.7	1.1	2, 6
H. spinulosus scabrellus (*Rose 1697*)..	25 ×20.5	5.1	2.0	12.5	4.8	2.0	30.5	5.1	2.4	2, 4, 6
§PRIONOPSIS										
H. ciliatus (*Ferris & Duncan 3315*)...	26	4.0	2.8	16 ×13.7	5.0	2.8				2
§PYRROCOMA										
H. croceus typicus (*Colo. Agr. Coll. 3234*)	29.1×25.8	5.9	3.4	14.8× 3.7	4.6	2.8				
rior §STENOTOPSIS										
H. linearifolius interior (*Eastwood 2795*)	25.1×22.8	4.6	1.7				29.6	4.7	1.7	4, 6
§STENOTUS										
H. lanuginosus typicus (*Howell* in 1885).	27.4	5.4	2.6							4
(*Kelsey* in 1890)..	23.9×21.6	4.2	1.7	10.1	3.4	1.4				
(*Cusick 3282*)....	26.2×24	4.6	2.3				34.2	4.8	2.3	2, 4
(*Leiberg 2139*)....	28.5×29.6	3.8	1.7	11.4	4.0	1.7				
H. lanuginosus Andersonii (*Macbride & Payson 3781*).....	25.1	3.9								4
H. stenophylus (*Cotton 346*)	26.8	4.4	2.3	10.8	4.0		35.3	5.7	2.3	6, 9
H. MacLeanii (*Tarleton 51*).....	27.5×25.1	4.4	2.3	11.9	4.6	2.3	35.6	4.0	2.3	4, 6
(*Gorman 1002*)....	24 ×21.5	4.6	2.3				30.5	4.6	2.3	4, 6, 8, 12
H. acaulis typicus (*Baker 987*)	27.4×23.9	4.8								4, 6
H. acaulis glabratus (*Nelson & Macbride 1914*).....	27.9	4.2	2.5				33.6	4.0		6
(*N. & M. 2173*)...	23.4	4.2	2.3							
(*Gooding 1111*)...	23.9	5.8	2.3							0
§ISOCOMA										
H. Hartwegi.....	24.5	4.5	2.0	12.5	4.8	2.3	28.	4.8	2.3	6
§ERICAMERIA										
H. ericoides (*Elmer 4025*).....	25.6	5.0	2.0	9.1	4.2	1.7	30.8	4.6	2.6	4, 6
Fresenia fasciculata (*Bolus 1872*).....	31.5	5.6	2.3				40.5×38.5	5.7	2.3	4, 6
Erigeron strigosus...	18.2	3.2	2.0							4, 6, 8, 9, 12

positae it is characteristic of the grains of *Boussingaultia baselloides* H. B. K. and *Nerium Oleander* L., and constitutes a large proportion of the grains of *Rumex Acetosella* L. and *Fraxinus americana* L. It is described by Fischer (1890) for the pollen of *Epiphyllum truncatum* Haw. With furrows united following a zigzag course it is common in the pollen of *Limnia spathulata* (Dougl.) Heller, and appears to have been described by Von Mohl (1835) for *Hypericum perforatum* L, though his description leaves some doubt as to the exact form found by him.

Hexacolpate grains. When grains have six furrows, their usual configuration is such that they are equally distributed over the surface, with their long axes converging towards four centers, which are triradiate and equally spaced (fig. 4). This arrangement is, perhaps, best visualized by saying that the six furrow axes correspond to the six edges of a tetrahedron, and the points of convergence correspond to the four solid angles of such a figure (fig. 15). This configuration of furrows was observed by Von Mohl (1835, p. 225) in the pollen of several species of *Corydalis* and described by him as tetrahedral: 'Toute la surface des grains se trouve ainsi partagée par six fissures en quatre triangles, ou en d'autres termes, les bandes de ce grain forment les arêtes d'un tétrahèdre'. It was also described and illustrated by Fritzsche (1837, pl. 6, fig. 5) in the grains of several species of *Corydalis*, and of *Basella*, and likewise regarded by him as the tetrahedral arrangement, 'Mit sechs den Kanten des Tetraëders entsprechenden Spalten' (p. 724).

When a hexacolpate grain is observed in such a position that one furrow is exactly uppermost, focussing down, if the grain is sufficiently transparent, will always reveal another furrow on the lower side, with its long axis directed at right angles to that of the upper; the four other furrows will be barely visible bending over the limb—the boundary of the median optical plane—(fig. 16), but their four germinal pores can generally be seen bulging at four points equally spaced on the limb. If, on the other hand, the grain be so oriented that one of the centers of convergence is uppermost (fig. 15), the three converging furrows will be almost wholly in view directed radially. And if now the microscope be focussed on the lower surface, the three other forrows will be seen with their long axes directed tangentially, forming an equilateral triangle, and with their three apertures alternating with the three above.

This tetrahedral form of a hexacolpate grain is one of the commonest atypical forms. In the present group it has been found in thirteen specimens representing twelve different species. In *Haplopappus acaulis glabratus* it was found in the Nelson and McBride specimen, but not in the Gooding specimen. It was also found in the only specimen examined of *H. acaulis typicus* (table 1). It is likewise found here and there among almost all groups of the Compositae, and is the characteristic form of the grains of *Dahlia*. I have examined the pollen of numerous unnamed varieties of the cultivated dahlia (*Dahlia variabilis*) and that of several natural species, and found their grains to be invariably hexacolpate with furrows in the tetrahedral arangement.

Outside of the Compositae, besides being characteristic for *Basella* and *Corydalis*, hexacolpate grains of this configuration are found in *Nerium*

Oleander L., *Talinum multiflorum* Rose and Stand., and occasionally in *Salpiglossis sinuata* Ruiz and Pavon. Those of the later are of particular interest because they suggest an explanation of the origin of such forms. The grains of this species of *Salpiglossis* are shed united in tetrads, generally tetrahedral in arrangement, and with all four grains tricolpate, with a furrow and a germinal pore at each of the three points of contact (Fischer, 1890; Wodehouse, 1929). Occasionally, however, some tetrads are found which are not exactly in the tetrahedral arrangement, but more or less tetragonal or rhomboidal, with some of the cells making only two points of contact with their neighbors. Such an arrangement frequently induces irregularity of form; one of the most usual for grains making two points of contact, if they are about one quarter of the circumference apart is the presence of four furrows with germinal pores, two at the points of contact and two others exactly opposite, as in the ordinary tetracolpate configuration (fig. 13). Such tetracolpate forms are fairly common among the irregular grains of *Salpiglossis*; but occasionally they are further modified by the possession of two more furrows without germinal apertures, on opposite sides of the grains and so arranged that they complete the tetrahedral hexacolpate configuration (figs. 15, 16). Thus it appears that both the tetracolpate and hexacolpate furrow configurations may arise when grains make two instead of three points of contact in the tetrad.

Hexacolpate grains are occasionally found with their furrows in a configuration which is not related to the tetrahedral. In this arrangement the furrows converge in pairs towards six centers, which are thus bilateral, instead of triradiate (fig. 20), but with angles of convergence at least approximating 120°. This arrangement suggests that this form may be regarded as a derivative from the nonacolpate configuration, to be described next, and which likewise has six centers of convergence; and bears the same relation to the nonacolpate form that the tetracolpate configuration bears to the ordinary hexacolpate type. But this form is rare and is usually accompanied by ugly distortions of the grains, rendering them extremely difficult of analysis; usually some of the furrows lack apertures and are fused at one or more of the centers of convergence, thus traversing a more or less discontinuous course around the grain in each hemisphere between the equator and poles. Quite frequently grains are found with just two furrows completely encircling them in the position of the tropics on the terrestrial globe, and I believe such zonate furrows represent the complete fusion and flattening out of the convergent angles of the six furrows of this form of hexacolpate configuration.

This type of hexacolpate grain, which is perhaps best regarded as a nonacolpate derivative, is found occasionally in the pollen of *H. MacLeanii*

(*Gorman 1002*); and its zonate derivative, which is probably not any commoner, but is much more easily recognized on account of its striking appearance, is found in the pollen of *H. stenophyllus*, and outside of the genus *Haplopappus*, in the pollen of *Artemisia spinesens* D. C. Eaton in the Anthemideae, and of *Limnia spathulata* (Dougl.) Heller in the Portulacaceae.

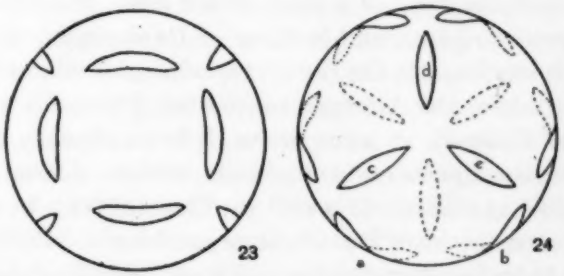
Nonacolpate grains. When grains have nine furrows they are equally spaced over the surface, and are so arranged that their axes converge towards six centers, which are triradiate (figs. 2, 5). This form bears the same relation to a form of pentahedron that the hexacolpate bears to the tetrahedron. This pentahedron is a right triangular prism of which three sides are equal squares and two, which are opposite, are equal equilateral triangles. In the nonacolpate grain there are three viewpoints which show the four furrows with their axes forming the sides of a square (fig. 18). Focussing down from any one of such reveals four more furrows curving around the limb of the sphere and converging towards the two ends of the ninth furrow, which subtends the upper square and is parallel to two of its sides. There are two views which show the axes of three furrows forming a triangle (figs. 5, 17). Focussing down from one of these brings into view three other furrows forming a triangle on the lower surface, and exactly subtending that above; the three remaining furrows are seen curving over the limb from the angles of one triangle towards the corresponding angles of the subtending triangle. This type of grain is not common, having been found thus far, among the Astereae, in the pollen of only two species, *Haplopappus stenophyllus* and *Erigeron strigosus* Muhl., but is fairly abundant in the latter (table 1). Outside of this group it is occasionally found in the pollen of *Artemisia gnaphaloides* Nutt. and *Rivina humilis* L., and is frequent among the grains of *Talinum multiflorum* Rose and Stand. This type of furrow arrangement is stated by Von Mohl (1835, p. 225) to characterize some of the grains of the pollen of *Corydalis lutea* DC., of which he says 'le graine représente un prisme triangulaire dont les faces latérales sont bombées, aussi bien que les terminales.'

The nonacolpate type, besides giving rise to a certain form of hexacolpate, and through this to the zonate type as noted above, apparently also gives rise to a curious half-zonate form (fig. 22), by the dropping out of two furrows and the fusion of those remaining at their resulting bilateral centers of convergence. I have not yet found grains of this form among the Astereae, but they are of frequent occurrence among the pollen of *Limnia spathulata*, and it is likely that a further search will bring them to light among the Astereae and elsewhere among the Compositae.

Octacolpate grains. When grains have eight furrows they present a very

unusual symmetry; the axes of the furrows converge towards six centers: four are triradiate, and two bilateral (figs. 3, 19). If such a grain is oriented under the microscope with the four triradiate centers visible in the upper hemisphere, four furrows will be seen in the position of the sides of a square. Focussing downward will bring into view four other furrows appearing to start on the limb at the four angles of the square and converge in pairs towards two close but discrete centers in the lower hemisphere.

This form may be regarded as a derivative of the nonacolpate through the omission of one furrow and the closing in of the others to partially occupy its space. Occasionally the two bilateral centers approach very closely or actually coincide, producing a single tetraradiate center, but more often they are separated, presenting an appearance similar to that shown in figure 9 of a tetracolpate grain.



Figs. 23, 24. 23. Dodecacolpate: twelve furrows converging towards eight centers corresponding to the eight corners of a cube; viewed with one of the spherical squares uppermost. 24. Dodecacolpate, viewed with one of the centers of convergence uppermost.

The octacolpate form is rather rare; it has been found only in a few grains of *Fresenia fasciculata* Bolus and *Erigeron strigosus*. Outside of the Astereae, it is common in pollen of *Artemisia spinescens* and *Talinum multiflorum*.

Dodecacolpate grains. When grains have twelve furrows they are equally spaced and so arranged that their axes converge towards eight centers which are triradiately symmetrical, the furrows dividing the surface of the grain into six squares (figs. 1, 23, 24). This form bears the same relation to a cube that the hexacolpate form bears to the tetrahedron, and that the nonacolpate form bears to the right triangular prism. It has been admirably described by Fritzsche (1837) for the pollen of *Talinum patens* Willd., in which it is clearly and beautifully seen on account of the absence of spines, and the transparency and regularity of the grains. As Fritzsche says (p. 725), 'Die Anordnung der Spalten ist auch hier höchst regelmäs-

sig, indem sie den zwölf Kanten eines Würfels entsprechen; sie sind von ziemlich grosser Ausdehung und theilen die Exine in sechs viereckige, mit den Ecken zusammenhängende Stücken.'

If such a grain is examined with any one of the centers of convergence exactly uppermost (fig. 24), focusing downward will bring into view another center exactly below but with its radii alternating with those of the center above. Or if the grain is oriented so that the axes of the furrows on the upper surface form a square (fig. 23), focusing down will bring into view another square exactly subtending the one above, and four other furrows will be seen bending over the limb from the angles of one square towards the corresponding angles of the other square. In this form the twelve furrows are never all occupied by pores; usually only four pores may be counted.

The dodecacolpate type of grain is rather rare. It occurs among the grains of *Erigeron strigosus*, and in those of *Haplopappus MacLeanii*, in which species it was found in the Gorman specimen but not in the Tarleton specimen. Outside of the Astereae, besides being found in the grains of some species of *Talinum*, as noted above, it is occasionally found in the pollen of *Artemisia spinescens* and, in its various derivatives, in the pollen of *Liminia spathulata*; it is said by Franz (1908) to characterize the pollen of some species of Portulacaceae, and is also said by Von Mohl (1835, p. 225) to be found among the pollen of *Corydalis lutea* and *Clerodendron paniculatum* L.

DISCUSSION AND CONCLUSIONS

In seeking phylogenetic characters among pollen grains it is necessary to keep in mind the fact that pollen grains are single cells, and to remember that 'the fate of a cell is strictly a function of its position plus its own independent organization with the resulting capacity for interaction with its fellows' (Harper, 1908). Not all of its character is the result of hereditary endowment; fully as much is acquired from contact with its neighbors and is due to whether its position was this or that in the tetrad. Of pollen truly we may say with Nägeli (1842) 'Die richtige Erkenntniss einer Sache beruht auf der Kenntniss ihrer Vollendung und auf der Kenntniss ihrer Entstehung.' When a pollen cell comes fully matured from the anther it bears the record of much of its past history, so that by studying the details of its structure in its final and completed form much may be learned of its beginning—of its origin by bipartition with rectangular intersection, and how completely or incompletely successful it was in attaining to the tetrahedral or least surface configuration. For each grain bears imprinted upon it, not only the stamp of its own independent organization, but like-

wise the marks of its interactions with its neighbors during growth, recorded in part, after its own particular fashion, but guided in principle by the physical laws governing the materials of which it is composed.

Thus it is that in attempting to use pollen characters in classification we must clearly distinguish between those which are of the grain's own independent organization (emphytic) and those which are the result of its interactions with its fellows (haptotypic). In *Haplopappus* those of the first category are the spine-length, spine-interval or frequency, and surface texture, and, to a certain extent, the size. Whereas the characters which are the result of the cell's interactions with its fellows are the number of germinal apertures and furrows, and their configurations. These two characters are governed to a certain extent by chance relations with their neighbors and subject to such simple physical forces as those of surface tension, mechanical stress, friction and cohesion, but which are responded to in a characteristic way by the development of a certain type of furrow of a rather definite length, which is again an emphytic character, representing the cell's specific capacity to respond to stimuli.

In their emphytic characters the grains of all species of *Haploppapus* and most of the Astereae are essentially alike, showing rather less variation than would be expected among closely related species of a genus. In fact, the observable differences are so slight that they do not admit of further analysis, and may be dismissed by saying that their monotonous similarity throughout the genus *Haplopappus* and most of the Astereae abundantly sustains the idea of genetic continuity and close interrelationship among the species.

Haptotypic characters, on the other hand, are various, consisting of the number and arrangement of furrows; though these tell us nothing of genetic relationships, a study of the arrangement of the furrows of various numbers reveals certain underlying laws controlling their configurations, which may be deduced as follows. It has already been shown that when a pollen grain forms in the tetrahedral arrangement, it makes three points of contact—one with each of its three neighbors of the tetrad— and consequently acquires three furrows equally spaced around the equator (Wodehouse, 1929). This explains the tricolpate form and triradiate patterns which characterize the majority of dicotyledonous pollen grains. But pollen grains do not always have three furrows, nor do they always form in the tetrahedral arrangement. When they form in some other arrangement with two unsymmetrical points of contact, two furrows are formed with orientation on the two points, but the cell maintains its symmetry in spite of this by the formation of symmetrically balancing furrows. Asymmetry in space relations among pollen grains, and perhaps among all

cells, is avoided as far as possible. This is obviously a matter of physical equilibrium, for, as Thompson (1917, p. 209) notes, 'in every symmetrical system any deformation that tends to destroy the symmetry is complemented by an equal and opposite deformation that tends to restore it.'

Among the grains of the Astereae are many with four furrows which undoubtedly arose in this fashion; but there are even more grains with six and other numbers of furrows.

We have noticed that in all the various configurations assumed by the furrows, they tend to converge towards each other in threes with equal angles of convergence, which consequently approximate 120°. This may be stated as the law of equal triconvergent angles. Occasionally, it is true, one of the furrows may be absent, leaving only two furrows converging towards a center, but in such cases one of the two remaining angles tends to be 120°. This law appears to be practically universal for grains which are spheroidal, as are those of the Astereae, but does not apply to grains which are much flattened. Furthermore, when a furrow is missing from a center of convergence, the two remaining have a strong tendency to coalesce at their ends, or sometimes such a condition may even lead to the total collapse of such defective configurations, resulting in sadly distorted and misshapen grains, suggesting an unstable condition at such biradiate centers. From this it becomes evident that, unless a grain have three furrows, or some multiple of three, it must have some biradiate centers of convergence, with their resulting lack of stability. 'Die ganzen Zahl hat Gott gemacht; alles anders ist Menschenwerk.'

The interesting relation between the various furrow configurations and certain polyhedra will become clear if we consider the characters of polyhedra in relation to the sphere as follows. The tetrahedron, for example, which is the simplest polyhedron, is bounded by four equal faces, each of which is an equilateral triangle with angles of 60°. If a sphere be circumscribed about a tetrahedron and the four vertices joined by the shortest possible lines in the surface of the sphere, subtending the edges of the tetrahedron, these lines will be arcs of great circles, and will intersect at the four vertices in such a way as to make three equal convergent angles at each, and incidentally, they divide the surface of the sphere into four equal spherical triangles whose angles are 120°. The arrangement of such lines corresponds precisely to the furrows of an hexacolpate grain. In the same way if a sphere be circumscribed about a cube and the arcs of great circles passed through the vertices of the cube so as to correspond to its edges, these arcs will correspond in position to the twelve furrows of a dodecacolpate grain, and will divide the surface of the sphere into six spherical squares, whose angles, since here again there are three equal

and convergent at each of the vertices, are 120°. These are the kind of square pieces that Fritzsche meant when he said, in speaking of the furrows of the grains of *Talinum patens*, 'Sie . . . . theilen die Exine in sechs viereckige . . . . Stücken.' In this connection it must be borne in mind that polygons, whether they be triangles, squares, or pentagons, when drawn over the surface of a sphere so as to divide the surface into equal parts, must always have their angles equal to 120°.

If we write out the series of symmetrical furrow configurations known to occur in pollen grains, it is seen that to each of these corresponds a polyhedron; also some other interesting facts become evident.

NO. OF FURROWS	CORRESPONDING GEOMETRICAL FIGURE	NO. OF EDGES	NO. OF FACES
0	0	0	—
3	3 coincident straight lines	3	—
6	tetrahedron	6	4
9	right triangular prism	9	5
12	cube	12	6
15	pentagonal prism	15	7
30	pentagonal dodecahedron	30	12

As the number of furrows increases by steps of three the number of faces of the corresponding polyhedra increases by steps of one, which relation may be expressed by $E=3F-6$, where $E=$ the number of edges or furrows, and $F=$ the number of faces.

Obviously there can be no polyhedron corresponding to grains with no furrows. Grains with three furrows, according to this equation, would require a polyhedron with three edges and three faces. No solid geometrical figure can be constructed to correspond to this because three planes cannot enclose space, but three curved edges and three curved faces can enclose a space, as they do in the usual pollen-grain form of the majority of dicotyledons, the tricolpate grains in which three arcs of great circles divide the surface of the grain into three equal lunes.

The largest number of furrows so far encountered in the pollen grains of *Haplopappus* and the Astereae is twelve. The higher numbers of furrows are difficult to count because of the nature of the grains; so whether or not numbers higher in the series than twelve exist among them is still uncertain. Outside of the Astereae, however, fifteen furrows are reported by Fischer (1890, p. 56) for the grains of *Talinum patens* and *Montia fontana* L., in which he says that they form a five-sided prism, also in the pollen of *Platycapnos spicatus* [=*Fumaria spicata* L.] (p. 37). The next number which, so far as I am aware, is recorded in the literature is

thirty furrows described by Von Mohl for the grains of *Rivina brasiliensis* Nocca, *R. humilis* L., and *Fumaria spicata*. In the latter he states that the great transparency of the granular exine permits the distinction of areas marked off by the furrows and distributed in such a way that the whole surface of the grain is divided into pentagons which form a pentagonal dodecahedron (p. 225). A similar configuration is described for the grains of *Polygonum amphibium* L. and *Alsine media* by Fritzsche (1837, p. 725), who lays special emphasis upon the regularity of the pentagons and their arrangement. A similar figure is likewise described by Fischer (p. 56) for the grains of *Portulaca oleracea* L. and *P. grandiflora* Hook. Furthermore in the Portulacaceae the dodecahedron is said by Franz (1908, p. 33) to be the usual configuration for a large section of the family: 'Die Grundform des Pollens ist in der ersten grossen Gruppe, bei den Portulacoideae, das Pentagondodekaeder.'

The pentagonal dodecahedron with twelve faces and thirty edges fits into our series, fulfilling the requirements of $E=3F-6$, so it is not surprising that grains should be found with furrows conforming to this configuration. It is something more than a coincidence, however, that so many kinds of pollen grain exhibit the dodecahedron as the ground plan of their furrow arrangement, while apparently, if one is to judge from the literature reports, few, if any, exhibit the numbers of furrows intervening between fifteen and thirty. Why should the pentagonal dedecahedron be so favored among mathematical configurations, to the apparant total neglect of several simpler configurations involving fewer furrows? In the first place the pentagonal dodecahedron is a striking and unique figure. It differs from the prisms and other polyhedra which would accomodate the furrow numbers of our series between twelve and thirty, *in being perfectly regular*. It is one of the five possible regular polyhedra. All of its faces are regular pentagons, with all of their sides equal and all of their angles 108°, and all of their interfacial angles equal. The other regular polyhedra are the tetrahedron, octahedron, icosahedron, and cube. Of these only the tetrahedron, which is bounded by four triangles, and the cube, which is bounded by six squares, share with the pentagonal dodecahedron the convergence of three and only three edges and angles at their vertices. The octahedron and icosahedron present four and five convergent angles at their vertices, a condition quite incompatible with the triconvergent angular pattern of pollen-grain-furrow configurations; consequently they may be dropped from further consideration. As with the tetrahedron and cube, when the pentagonal dodecahedron is drawn over a sphere, that is to say when constructed with its faces of spherical pentagons instead of plane pentagons, the convergent angles will be equal and exactly 120°.

It thus becomes clear that perfect symmetry can only be attained when the furrows correspond in number and arrangement to the edges of a regular polyhedron having three equal convergent angles. It is such symmetry relations as these which account for the tetrahedron, cube, and pentagonal dodecahedron being favored members of the series.

If, on the other hand, we draw a right triangular prism over the surface of a sphere, equality of the three convergent angles at each of the centers of convergence cannot be attained, because in the plane triangular prism the angles of the equilateral triangles are 60° while those of the associated squares are 90°. When such a figure is adapted to the spherical curvature, and the edges take up the positions of arcs of great circles, the disproportion of these angles is further increased, though their total is now equal to four right angles. Thus we have a conflict between the law of equal triconvergent angles and the difference between the spherical values of a right angle and a 60° angle. When the angles of the polyhedron are small, as 60° and 90°, an adjustment takes place. This is accomplished in various ways; sometimes a compromise is struck by a shift of the furrows which bound the triangle a little out of the paths of great circles, tending to equalize the angles. If this is carried far, the grain sometimes shows a tendency to alter its shape, adapting the surface curvature to that of the furrows in such a way as to cause them to follow geodetic curves; the result is a slight bulge through the triangular faces. Such an adjustment, though common in the grains of some species outside of the Composite, appears not to be found in the grains of the Astereae; in these the adjustment is apparently made mostly at the expense of the equality of the triconvergent angles, with perhaps a little shifting of some of the furrows out of the paths of great circles. Seldom does the grain change its shape.

The scarcity of the 15-furrowed grains and the still greater scarcity or possibly entire absence of grains with furrows numbering between 15 and 30, is apparently due to the difficulty or impossibility of making such an adjustment. It appears that all four of the polyhedra missing from our list would have some hexagonal faces; and since the internal angle of a plane hexagon is 120°, that of a spherical hexagon must be appreciably greater than 120°, unless the hexagon is very small as compared with the sphere. This at once precludes the possibility of equal triconvergent angles. If there exist grains with furrow configurations corresponding to any of these missing numbers, they must be unsymmetrical and consequently less stable than those with the more perfect symmetry corresponding to the regular polyhedra which have equal triconvergent angles, and in which there is no conflict between the angles of different types of polygon.

There are only three of these, the tetrahedron, cube, and pentagonal dodecahedron.

The question now arises, what determines which one of these configurations shall be adopted by the grain? When a grain makes three points of contact in the normal tetrad, these points are equidistant and such a grain will acquire three furrows; but if it makes only two points of contact it may acquire a larger number. Information on this point is at present meager. We do know, however, that in the dividing chicory pollen grain, two points of contact can result in four furrows (Wodehouse, 1929). In the particular instance cited the four cells of the tetrad were all of the same size, but in the tetragonal instead of the tetrahedral arrangement. Further light is thrown on this point by a condition sometimes found in the grains of *Salpiglossis*. Its pollen is shed united in tetrads which are generally tetrahedral and with each grain tricolpate. Occasionally, however, one finds tetrads in which one of the cells did not quite achieve the tetrahedral position, though approaching very close to it but making only two points of contact. Such cells may acquire four furrows with apertures, converging in pairs at 120°; or more frequently two other furrows, generally without apertures, are thrown in between the two biradiate centers. These bear a striking resemblance to the polar furrow or 'Brechungslinie' which is nearly always developed in segmenting eggs when four cells are formed in contact and which would otherwise all meet at a point. In the same way that the 'breaking line' in the segmenting egg separates the unstable tetraradiate center into two stable triradiate centers, thereby restoring the stability of the segmenting egg, these two connecting furrows in the pollen grain of *Salpiglossis* each join together two unstable biradiate centers, and in so doing complete the tetrahedral hexacolpate configuration, and thereby restore the symmetry and stability of the grain.

Facts do not carry us much beyond this point, but furnish some ground for further speculation; for if two contact points can induce the formation of three, four, or six furrows, there seems no reason why two contact points could not likewise induce the formation of nine, twelve, or more furrows, the choice depending upon the distance apart of such points in relation to the periphery of the grain. For example, if the formation of two furrows should be induced by contacts in such a position on the limb, as at *a* and *b* (fig. 24), that four more would be required to symmetrically balance them on the limb, these six furrows would converge in pairs and thus establish six unstable biradiate centers of convergence. From such an arrangement stability could be recovered and symmetry completed by the formation of three connecting furrows as *c*, *d*, *e* in each hemisphere. Our grounds for assuming that three connecting furrows would form under

these conditions to join the six furrow ends in each hemisphere are again based upon observations in developing embryos; for here when six cells are formed in contact so that they would otherwise meet at a point, they are always separated by the formation of three intermediate walls, or breaking lines, which are themselves frequently triradiate in arrangement, and form with the walls of the six cells three more triradiate centers with all the angles 120°.

The distance apart of the initiating points must depend partly upon the position of the grain in its tetrad, but to a larger extent upon its size in relation to its neighbors. It is obvious that a shifting in the tetrad may change the distance apart of the contact points, but much larger relative differences are brought about by an increase in the size of the grains. Thus it happens that normal sized grains may occasionally bear four or six furrows, while the giants nearly always bear four, six, or larger numbers of furrows, and likewise grains with supernumerary furrows are nearly always giants. It is interesting and perhaps not without profit, to speculate further as to the origin of the furrows. The unequivocal insistence upon the 120° angle and the almost equal insistence upon the triradiate center of convergence of the furrow axes suggest that the furrows are the expression of stresses,—whether they be pressure or tension, the orientation would be the same. In a plane surface, pressure between objects of similar size and offering similar resistence to the pressure results in an hexagonal configuration with internal angles of 120°. So familiar is this configuration that it is always recognized at once as the result of pressure. In soap films the configuration likewise tends to be hexagonal and with the same insistence upon the 120° angle, and we recognize it at once as the result of tension.

On the sphere hexagons of finite size are incompatible with equal convergent angles between furrows, for reasons which we have already seen. In the case of the segmenting embryo it is well known that the arrangement of the cells is brought about by the tendency to assume least surface configurations, which in turn is the result of surface tension, and as Plateau has shown, is equally the property of oil drops and soap films. Consequently it is reasonable to suppose that the furrow configurations are brought about by similar forces. But if we recognize the hexagonal system with its internal angle of 120° as denoting relations of stress in a plane surface, by the same token we should be able to recognize triangles, squares, and pentagons with angles of 120° on a spherical surface as likewise denoting relations of stress. This being so, it follows that supernumerary furrows and their configuration on the surface of pollen grains are due to stresses set up in the grain by contact stimuli received at two points in

the tetrad. And the particular type of configuration is determined by the relative distance apart of the two points.

Most of the materials used in this study were obtained from the herbarium of the New York Botanical Garden; and the author desires to thank members of the staff for courtesies in connection with the use of the herbarium and library.

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ADDENDUM

The mathematical basis of the furrow configurations of pollen grains, as set forth in this paper, has received a remarkable confirmation by the work of P. M. L. Tammes,[1] which has appeared while the present communication was in the hands of the printers. Dr. Tammes' study of the various arrangements of germinal apertures, as distinct from furrows, leads him to conclusions nearly the same as mine regarding their spatial configuration. His analysis of them is based upon point systems on the surface of a sphere, and the similarity of his conclusions ot those of my

[1] TAMMES, P. M. L. On the origin of number and arrangement of the places of exit on the surface of pollen grains. 82 p. *f. 1–21+pl. 1–3.* Amsterdam, J. H. de Bussy, 1930. (Apparently issued in March as a doctor's thesis; indicated as an extrait from Recueil des Travaux Botaniques Néerlandais vol. 27, 1930, but probably published separately in advance, since issues of this journal for 1930 have not yet been received in New York libraries.)

paper above goes to show that the underlying mathematical principles are basic, and may be expressed either in terms of the geometry of polyhedra as I have indicated, or in terms of the geometry of the sphere, as has been done by Tammes.

Explanation of plate 1

All figures were drawn from studies made with a Zeiss 2 mm. apochromat objective, n.a. 1.3, and paired 10× binocular eye pieces. The measurements given are those of the average diameters. The sizes of the drawings are chosen to best display the characters of the grains, and do not bear a constant relation to the sizes of the grains.

Fig. 1. Pollen grain of *Haplopappus MacLeanii* Brandegee (*Gorman 1002*) 27μ diam. Dodecacolpate. Four furrows are shown on the upper hemisphere converging towards four centers. Four other furrows exactly subtend these, forming a square on the lower hemisphere; and four others bend over the limb, converging towards the corresponding angles of the upper and lower squares.

Fig. 2. Pollen grain of *H. MacLeanii* (*Tarleton 51*) 30.8μ diam. Nonacolpate. Three furrows are seen converging towards a center in the upper hemisphere. The germinal pores of three of the other furrows are to be seen bulging over the limb on the left side of the grain. The positions of the furrows in this case correspond to the edges of a right triangular prism, cf. fig. 5.

Fig. 3. Pollen grain of *Erigeron strigosus* Muhl. 19.8μ diam. Octacolpate. Four furrows are shown in the upper hemisphere, converging towards four centers and forming a square. Four more furrows, one arising from each of these centers, bend over the horizon and converge in pairs towards two more centers in the lower hemisphere.

Fig. 4. Pollen grain of *H. acaulis typicus* Hall (*Baker 987*) 24μ diam. Hexacolpate. Three furrows, two with pores and one without, are seen converging towards a center in the upper hemisphere, but with their opposite ends disappearing over the limb into the lower hemisphere. Three more furrows, in a triangular arrangement converge towards the ends of these furrows in the lower hemisphere, thus giving four centers of convergence, relative in position, to the four solid angles of a tetrahedron. This configuration of six furrows is known as *tetrahedral*.

Fig. 5. Pollen grain of *H. stenophyllus* Gray (*Cotton 346*) 27.5μ diam. Nonacolpate. As seen in this view, three furrows form a triangle in the upper hemisphere. These are subtended by three more in the lower hemisphere, while three others bend over the limb, converging towards the corresponding angles of the two triangles, cf. fig. 2.

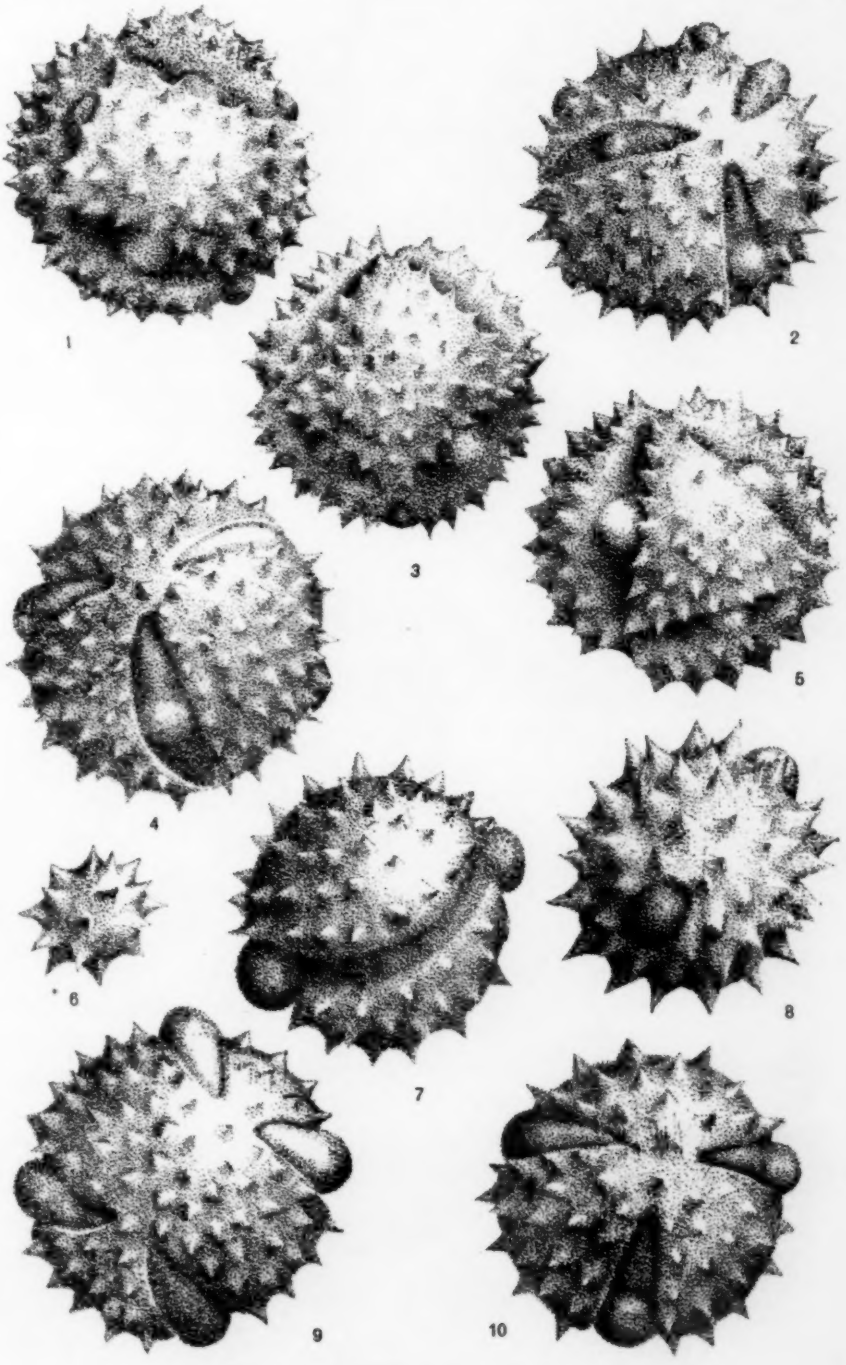
Fig. 6. Pollen grain of *H. MacLeanii* (*Tarleton 51*) 10×11μ diam. Drawn to the same scale as the grain of *Euhaplopappus*, fig. 10.

Fig. 7. Pollen grain of *H. lanuginosus typicus* Hall (*Cusick 3282*) 24.2μ diam. Dicolpate, with furrows opposite and completely fused.

Fig. 8. Pollen grain of *H. acaulis glabratus* (D. C. Eaton) Hall (*Gooding 1111*) 23.1μ diam. Acolpate. No trace of furrows is found yet these grains appear to be normal in every other respect.

Fig. 9. Pollen grain of *H. MacLeanii* (*Gorman 1002*) 27.5×29.7μ diam. Tetracolpate. Four furrows are seen converging in pairs towards two centers in the upper hemisphere. They bend over the limb and, changing partners, converge towards two centers in the lower hemisphere which are alternate with those of the upper.

Fig. 10. Pollen grain of *H.* (*Euhaplopappus*) *chrysanthemifolius* (Less.) DC. (*Holway* in 1919, ex herb. Gray) 30.8×28.6μ diam. Tricolpate. The normal form, and typical of the majority of the grains of nearly all species of *Haplopappus*.



WODEHOUSE: POLLEN OF HAPLOPAPPUS

UNIV. OF MICH.

The relationships of Paulownia

DOUGLAS HOUGHTON CAMPBELL

(WITH THREE TEXT FIGURES)

On the campus of Stanford University are several specimens of *Paulownia tomentosa* (Thunb.) Steudel, which in the early spring, before the leaves appear, at once attract attention by the profusion of very showy purple flowers. Somewhat later *Catalpa speciosa* Warder is almost equally conspicuous, and immediately invites comparison with *Paulownia*, which in habit is extraordinarily like *Catalpa*, as it is in the form of the flower and inflorescence. The fruit differs in shape from that of *Catalpa*, but closely resembles that of some other Bignoniaceae, as do the winged seeds.

The layman would immediately assume that the two trees were closely related; but on referring to the manuals, and to such authoritative works as the *Natürlichen Pflanzenfamilien* of Engler and Prantl, he is surprised to find *Paulownia* assigned to the Scrophulariaceae, instead of to the Bignoniaceae where he expected to find it. Apparently the only point in which it differs from the typical Bignoniaceae is the presence of endosperm in the seeds, a condition which is characteristic of the Scrophulariaceae.

Convinced that this single character was not sufficient reason for removing *Paulownia* from its obvious relationship with the Bignoniaceae, I investigated the history of its nomenclature, and I am greatly indebted to Dr. F. W. Pennell, who has furnished me much information as to the early history of *Paulownia*.

The tree was first named *Bignonia tomentosa* by Thunberg,[1] who evidently regarded it as a member of the Bignoniaceae. The name *Paulownia* was given by Siebold and Zuccharini,[2] who called it *Paulownia imperialis*. It was Endlicher[3] who transferred it to the Scrophulariaceae because of the presence of endosperm, and all subsequent taxonomists, until very recently, have accepted his conclusion. Examining the more recent literature, my attention was called to a paper by Dr. N. L. Britton,[4]

[1] THUNBERG, Flora Japonica 252. 1784.

[2] SIEBOLD AND ZUCCHARINI, Flora Japonica 1: 27. 1835.

[3] ENDLICHER, Genera Plantarum. 678. 1839.

[4] BRITTON, N. L., Jour. N. Y. Bot. Gard. 21: 72–73. 1920.

in which the view was expressed that *Paulownia* should be replaced in the Bignoniaceae. Dr. Pennell also wrote me that this view had been expressed recently by some European botanists.

Thinking it might be worth while to examine critically the seed structure, microtome sections were made of the ripe seeds which are freely produced at Stanford. It will be seen from the figures (fig. 1) that, while

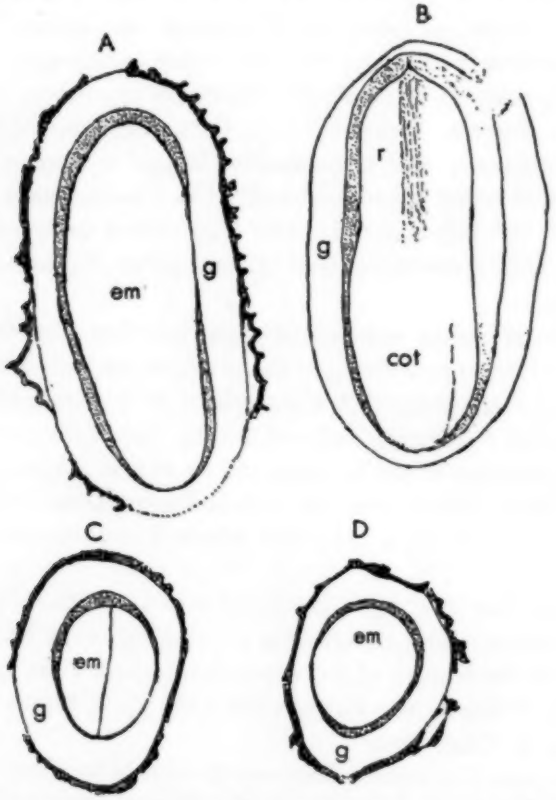


Fig. 1. A. Longitudinal section of the seed of *Paulownia*; *em*, embryo; *g*, endosperm. B. Longitudinal section of the embryo and endosperm, the latter somewhat broken in sectioning. *r*, radicle; *cot*, cotyledons. C. Transverse section of seed, passing through the cotyledons. D. Another section of the same embryo, passing through the radicle. All figures magnified about 60 times.

it is true that some endosperm is present, nevertheless the embryo is much larger than in any of the Scrophulariaceae—at least any of which I could find figures (fig. 3). Figure 2 shows sections of the seed of a *Pentstemon*, probably a hybrid, used freely as a garden flower in California.

Since the endosperm in *Paulownia* is much less abundant than in the Scrophulariaceae, and inasmuch as in all other essential characters it

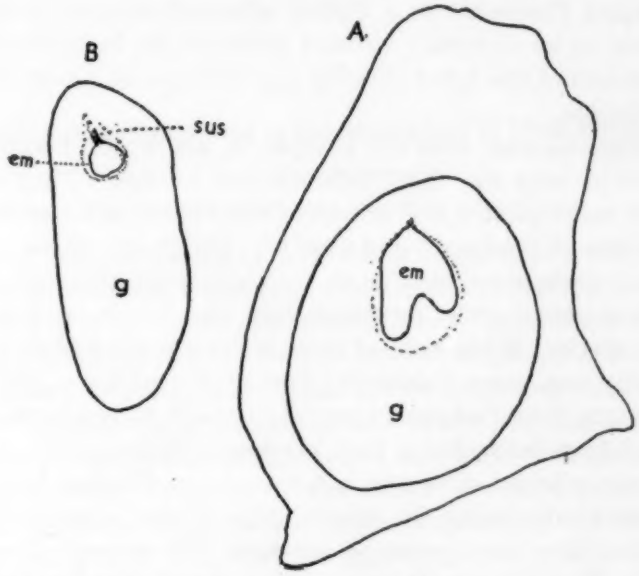


Fig. 2. A. Longitudinal section of seed of *Penstemon* sp. *em*, embryo; *g*, endosperm. B. Embryo-sac from a younger seed. The embryo shows a conspicuous suspensor, *sus*. ×about 60.

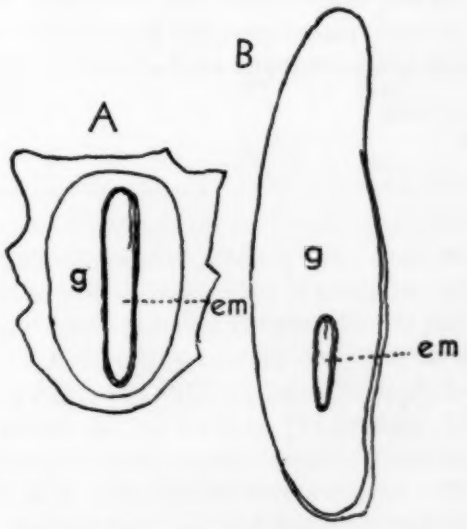


Fig. 3. A. Longitudinal section of seed of *Antirrhinum majus*. B. *Veronica arvensis*. After Chatin. (Ann. Sci. Nat. Bot. V. **19**: **pl. 3. f. 13, 29.** 1874).

agrees with the typical Bignoniaceae, it is much more likely that we should regard *Paulownia* as a slightly aberrant member of that family rather than as an extremely isolated genus of the Scrophulariaceae, no other members of the latter showing any evidence of a near relationship with *Paulownia*.

The Bignoniaceae, with few exceptions, are woody plants—some of them trees of large size like *Paulownia* and *Catalpa*. They are mostly tropical or subtropical, a few extending into the warm temperate regions, as in the case of *Paulownia* and *Catalpa*. The Scrophulariaceae are predominantly herbaceous, and have their maximum development in the temperature zones, even extending into the Arctic, and with many mountain species. While some of them in the warmer regions are more or less shrubby, e.g. some Californian species of *Pentstemon* and *Diplacus*, and numerous New Zealand Veronicas, the only truly aborescent forms, so far as I have been able to find, are two or three species of *Veronica*, which attain a height of twenty feet, or occasionally more.[5]

Wettstein,[6] discussing the relationships of the Scrophulariaceae, indicates that they have points in common with several other families, notably the Bignoniaceae. It is conceivable that the two families may have been derived from a common stock; but which (if either) is the older it is impossible to decide. It is possible that further study of the seed structure in the Bignoniaceae, especially among the few herbaceous genera, e.g. *Incarvillea*, may reveal other forms with endosperm, as in *Paulownia*.

In the Gesneriaceae, placed next the Bignoniaceae in the Engler and Prantl system, both albuminous and exalbuminous seeds occur.

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[5] CHEESMAN, T. F., Manual of the New Zealand Flora. Ed. 2. 1925.

[6] WETTSTEIN, R. v., Scrophulariaceae. ENGLER AND PRANTL. Die Natürlichen Pflanzenfamilien 4^{3b}: 48. 1895.

Induced alteration of sex in the male plant of Mercurialis annua

CECIL YAMPOLSKY

WITH PLATE 2 AND TWO TEXT FIGURES

Among the male plants of *Mercurialis annua* grown over a period of years, individuals are found that produce one or more female and hermaphrodite flowers. It has been established that besides the absolute males, graded expressions of the male sex are present, and such sex intergrades readily set seed. Male plants grown in the greenhouse show little tendency towards the production of flowers of a different sex. In one of the first trials of the male of *Mercurialis annua* 215 male plants produced a total of 17 seeds. From the cultures of 1915 grown in the open 29 of the 500 male plants produced female and hermaphrodite flowers. Including the cultures of 1915, a total of 790 male plants were under observation; these distributed themselves as shown in table 1.

TABLE 1

Number of male plants that produced seeds

NO. OF PLANTS	NO. SETTING SEED	NO. OF SEEDS	NO. WITHOUT SEEDS
12	2	8	10
36	1	7	35
167	1	2	166
500	29	283	471
75	2	4	73
Total 790	35	304	755

Since 1915 many hundreds more of male plants have been grown, and the number of individuals that produce other than male flowers has been augmented. In the year 1926, one out of every ten produced from one to several female and hermaphrodite flowers. A male plant may produce one to several fruits. A fruit may contain one, two, or three seeds. One of the plants in the culture of 1915 produced 93 seeds besides 90 additional female flowers which did not set fruit (Yampolsky, 1919).

For theoretical reasons it became desirable to ascertain how *Mercurialis annua* would react if subjected to severe shocks. The plants used were the offspring of the original male and female plants that have served as a basis for experimentation since 1914. The plants have been propagated in the greenhouses of the Department of Botany of Columbia University, where the experiments were carried on.

The following results deal with male plants in three groups of twelve, given the same treatment and grown under identical conditions. In each group six plants were severely pruned, only two or three small lateral branches being allowed to remain. The other six were kept as checks. In every case plants of the same age and of equal vigor were selected.

GROUP I (1927)

The plants selected were about four months old. They were of a uniform dark green; they produced countless numbers of male flowers and showed no evidence of female or hermaphrodite flowers. On the 15th of April six plants were severely pruned. The mutilated plants and six intact plants were placed under the same conditions and observed at regular intervals. For the first few weeks growth in the mutilated plants was at a standstill. Then they began to recover, sending out many side branches, and in the course of several months the vegetative growth had progressed appreciably. All the branches bore profuse numbers of male flowers. Two and one-half months after the injury four of the six plants showed one to several female and hermaphrodite flowers. The checks, however, although they maintained their vigor, produced only male flowers.

TABLE 2

Plants of Group I

PLANT	NO. OF SEEDS	
	June	July
1001[a]	4	2
1002	21	0
1003[b]	10	0
1004	9	0
1005	0	0
1006	0	0

[a] Plant 1001 produced one female flower which dropped off.
[b] Plant 1003 produced four female flowers which dropped off.

As set forth in table 2, four of the six mutilated plants produced a total of 44 seeds. Two mutilated plants failed to produce any seeds. The six check plants produced no seed. By the end of July all the plants had lost their vigor and they were discarded.

GROUP II (1928)

The plants selected were about four months old and of the same stock as those in Group I. Uniform plants were selected and they were carefully examined for female and hermaphrodite flowers. On January 5 six plants were severely pruned and the other six remained as checks. The first evidence of flowers appeared two months later and by that time the

mutilated plants had regained their full vigor. Only two of the six plants produced seed; each produced 4 seeds. The checks produced only male flowers. The plants were discarded in June without having produced any more seed.

GROUP III (1928)

The plants used were about four months old and of the same stock as the plants of the other group. Twelve plants of equal size and vigor were selected. At the time the experiment was started all the plants were examined and had produced only male flowers. On February 28 six of the plants were severely pruned leaving one, two, or three small lateral branches. The first evidence of sex reversal appeared exactly one month later; plant 103 produced twenty female flowers, beside the large number of male flowers. Plants no. 100 and 103 showed the most striking sex reversal judged by the relatively large numbers of female and hermaphrodite flowers that were produced all over the plant. Whereas in some of the mutilated plants in the other group only a few of the branches bore flowers of a different sex, in these two plants practically every branch produced hermaphrodite and female flowers and later fruit.

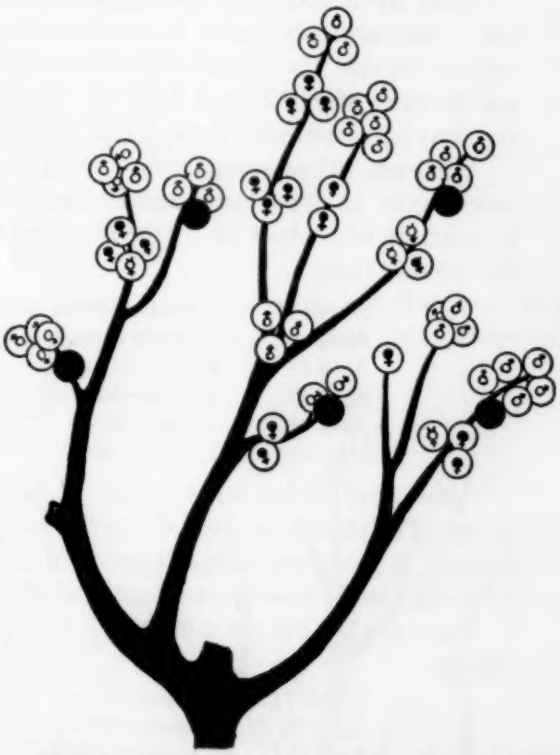

Fig. 1. Plant no. 100, showing male, female, and hermaphrodite flowers, as well as seeds—one and a half months after severe pruning.

Text figure 1 represents diagrammatically the whole plant no. 100 as it appeared on April 15, a month and a half after pruning. The plant by that time had recovered, and all its branches were vigorous and healthy. Male, female and hermaphrodite flowers are indicated by symbols, the fruits by black discs. The very many smaller male branches have not been indicated in the text figure. The complete story of sex reversal in this plant is as follows:

March 28	3 female flowers
April 4	3 fruits set—6 seeds
April 15	17 female flowers—4 hermaphrodite
April 23	2 fruits—5 seeds—one a three-carpelled fruit
April 26	5 female flowers
April 27	19 fruits—38 seeds
May 10	5 fruits—10 seeds

After April 26th only male flowers were produced. The plant grew into a vigorous male, and it was discarded at the end of June, when it was ten months old. The period of female and hermaphrodite flower production was between March 28 and April 26. During that time 29 female flowers and four hermaphrodite flowers and a total of 59 seeds were produced.

Plant no. 101 produced three female flowers on March 28. The plant was healthy in appearance and had recovered from the severe pruning. In contrast with plant no. 100 it produced fewer female and hermaphrodite flowers thus:

March 28	3 female flowers
April 4	7 female flowers—3 hermaphrodite flowers
April 15	8 fruits—16 seeds
April 17	5 fruits—10 seeds
April 23	1 female flower
May 10	1 fruit—2 seeds

After April 23 no other female or hermaphrodite flowers were produced. The plant grew into a vigorous male. It was discarded at the end of June. It produced during its period of sex reversal 11 female flowers and 3 hermaphrodite flowers and a total of 28 seeds.

Plant no. 102 did not differ much from plant no. 101. Its history is as follows:

March 28	2 female flowers
April 4	4 female flowers—1 hermaphrodite flower
April 15	7 fruits—14 seeds
	1 aborted female flower—1 female flower
April 17	1 fruit—3 seeded—1 aborted female flower

After that date only male flowers were produced. The plant then became completely male and died at the end of June. It had during its period of sex reversal produced nine female flowers (2 aborted) and one hermaphrodite flower and 17 seeds.

Plant no. 103, like no. 100, showed the greatest amount of sex reversal. Text-figure 2 represents diagrammatically the condition of the plant on April 15, a month and a half after pruning. Female and hermaphrodite flowers had appeared, and were distributed in all parts of the plant. It may be said of this plant, as well as of plant no. 100, that whatever the influence may have been which resulted in the formation of female and

hermaphrodite flowers, the influence showed itself all over the plant, and was not limited to any one part. The complete history of the plant is as follows:

March 28	20 female flowers
April 4	16 female flowers—4 hermaphrodite flowers
	4 fruits—4 seeds
April 15	22 fruits—44 seeds
	1 female flower—1 hermaphrodite flower
April 16	1 fruit—2 seeds
	11 female flowers
April 17	23 fruits—45 seeds
April 23	5 female flowers
April 26	4 female flowers
April 30	9 fruits—15 seeds
	4 female flowers—1 hermaphrodite flower
May 12	3 aborted female flowers
	5 fruits—9 seeds
May 22	2 fruits—3 seeds

After May 12 only male flowers were produced, and the plant was completely male after the last seeds were removed. The plant continued to grow until the end of June, when it was discarded. During the time of sex reversal the plant produced 64 female flowers, 6 hermaphrodite flowers, and 122 seeds. Some of the fruits bore 1 seed, 2 seeds, or 3 seeds.

Plate 2 shows two views of plant no. 103 taken at a time when the fruit was ripe and the plant at the height of its sex reversal. The general distribution of the fruit can readily be seen, and lends weight to the contention that all the branches have been thrown into a state of unbalance. The characteristic male inflorescences are obvious. The fruits are in the main borne at the end of peduncles. Some fruits are borne in the axils of the leaves.

Plant no. 104 of the same group as the other four produced ... pruning.

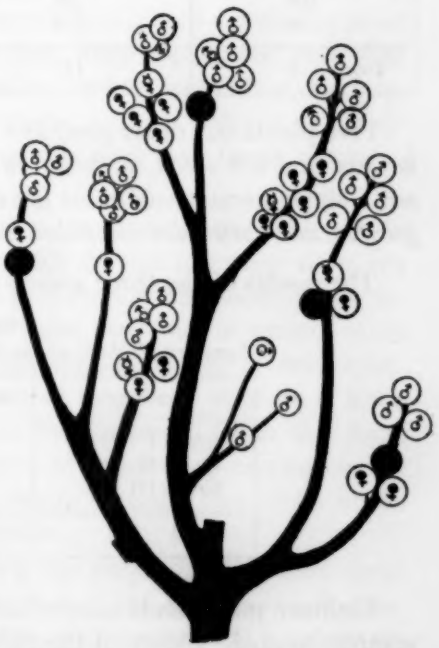

Fig. 2. Plant no. 103, showing male, female, and hermaphrodite flowers, as well as seeds—one and a half months after severe pruning.

but few female and hermaphrodite flowers. It was subjected to identical conditions and treatment as the others. It produced female and hermaphrodite flowers as follows:

March 28	2 female flowers
April 15	3 female flowers
	2 fruits—4 seeds
April 26	1 hermaphrodite flower—1 aborted female flower
	4 fruits—8 seeds

After that date only male flowers were observed. The plant produced six female flowers and one hermaphrodite flower, giving a total of 12 seeds. The plant grew into a healthy plant, and was discarded at the end of June.

TABLE 3

Summary of plants of Group III that produced seed

PLANT	FEMALE FLOWERS	HERMAPH. FLOWERS	SEEDS
100	29	4	59
101	11	3	28
102	9	1	17
103	64	6	122
104	6	1	12
Total 5	119	15	238

Five plants out of six produced 119 female flowers, 15 hermaphrodite flowers, and 238 seeds, as shown in table 3. The six check plants showed not a single hermaphrodite or female flower during their whole period of growth, and they were discarded at the end of June.

The results of the three groups combined are summarized in table 4.

TABLE 4

Summary of plants of the three groups that produced seed

NO. OF PLANTS	NO. SETTING SEED	NO. OF SEEDS
Group I (6)	4	44
Group II (6)	2	8
Group III (6)	5	238
Total 18	11	290

Eighteen male plants selected for vigor and uniformity of growth were severely pruned. Eleven of the eighteen responded by producing, besides their male flowers, varying numbers of female and hermaphrodite flowers. Eighteen check plants grown under the same conditions failed to produce other than male flowers. Sixty-one per cent of the mutilated plants pro-

duced seeds. Contrasting these results with the results obtained in the male cultures (table 1), it is quite evident that subjecting the male plants to a severe pruning results in a sex reversal. Of the 790 male plants only 35 produced seeds, amounting to a total of 304. Less than five per cent of the 790 produced other than male flowers. A very striking fact in these partial reversals was the transitoriness of the state. The severe pruning apparently resulted in unstable equilibrium which lasted for a short period, from one month to three months, and the plants returned to the completely male condition.

DISCUSSION

Examples of instability resulting in temporary or permanent alteration or reversal of sex are abundant in both the plant and animal kingdoms. The existence in nature of such phenomena as a combination of ovary and testis, of secondary sex characters of both sexes in the same individual, the transition from femaleness to maleness and the reverse, pistillody, staminody, cyclic alteration of sex certainly speak for the lability of sex.

In the plant world the array of evidence, experimental and observational, in the cryptogamic and phanerogamic flora, yields convincing proof of the non-fixity of sex. A variety of factors when applied and controlled have brought about a shift in the balance so that an erstwhile stable form has been toppled from its balance to assume another balance of a temporary or a permanent character. The new balance may result in temporary or permanent sex reversal.

The behavior of the mutilated male plants indicates that sex in *Mercurialis annua*, even in the forms which do not naturally show sex reversal, is subject to change. The fact that some of the males do not respond to the injury may indicate that in males which never produce other than male flowers a difference of a physiological character may exist. Those that did not respond to the pruning may have in them a more equalized balance between male and female elements. Those that have responded by producing varying numbers of female and hermaphrodite flowers may very well be physiological sex intergrades that never under normal conditions show their intergradation.

No attempt has been made to review the very large literature upon the subject of sex reversal in plants. In view of the extensive work done by Schaffner on a large number of forms, no attempt will be made to evaluate the results in the light of newer findings. The results obtained with *Mercurialis annua* are in harmony with those of Schaffner (1925) and with those of the Japanese investigator Maekawa (1924). The latter has

carried on an extended series of experiments with sex reversal in *Arisaema japonica* and has secured very striking results.

The results recorded here complement the genetic results obtained with *Mercurialis annua*. They further emphasize the assumption that in sexual union a balance is secured which results in morphological and physiological expressions. Since a number of balances are possible, some are more stable than others. For that reason sex intergradations exist. We have seen, however, that even stable balances may be disturbed by subjecting plants to so violent a shock as severe pruning. The period between pruning and the return to complete male expression was a time during which the plant was passing through a series of equilibria.

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Description of plate 2

Fig. 3. Upper portion of plant no. 103, showing the distribution of the fruits. The circles indicate the location of the fruits. A fruit may be one, two, or three parted. The commonest are the two parted fruits.

Fig. 4. Lower portion of the same plant, showing more of the fruits.

YAMPOLSKY: MERCURIALIS

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The tetrakaidecahedron in pseudoparenchyma[1]

ILLO HEIN

(WITH PLATE 3)

Lewis (1923, 1925, 1926, 1928) has several times given evidence that cells in masses tend to be typically tetrakaidecahedral. His conclusions have recently been supported by Matzke (1927), who demonstrated mathematically that the angles and faces of tetrakaidecahedra of equal volumes will coincide, and showed with models that such polyhedrons can be stacked without voids. The problems involved have been reviewed by Lewis (1928), Millis (1926), and Gross (1927), and the most recent summary of the literature has been given by Matzke (1927).

Studies in the past have been made on cork cells, elder pith, human epithelial, and adipose tissues, but no studies have been reported for the fungi. It is not very common to find cells massed in pseudoparenchyma under conditions favorable for a study of their typical form. I have recently found in mushroom beds a sclerotium, of which the species is as yet unidentified, which illustrates beautifully the form of such hyphal cells.

This sclerotium is the one which was used in my recent studies on concentric zonation in fungi (Hein, 1930). For the present report studies were made from Petri dish cultures of sclerotia. Small blocks of agar were imbedded in paraffin and sections cut in three planes perpendicular to one another.

The appearance of the sclerotium tends to conform in every respect, both in the shape of the individual cells and in the form of the structure as a whole, to well known expressions of the laws of surface tension. This is, however, due to the aggregated centric growth habit of the hyphae. The cells, with the exception of the somewhat flattened peripheral ones, are approximately similar in form in every plane, nearly isodiametric, and of fairly uniform size (figs. 1–3). The sclerotium as a whole is spherical or nearly so (fig. 5). Occasionally ovoid forms are encountered, but these have originated, as can be clearly shown in a series of early stages, by the fusion of two or more sclerotia.

There is no evidence of a filamentous arrangement of the cells in the

[1] Presented before the Botanical Society of America at Des Moines, December 31, 1929.

sclerotium, and in this respect the appearances are analogous to those in a froth.

A median section through a typical sclerotium showed that there were a little over 600 cells, and a count of their sides is given in table 1. Since it seemed that in a single section through a sclerotium there might be an insufficient number of cells for a fair average count, the number of sides of 2000 cells from five different but similar sclerotia were counted. The yields for the latter, as exhibited in table 2, give an average of even more nearly six sides per cell.

TABLE 1

600 sclerotial cells in median section

Number of sides....	3	4	5	6	7	8	9	average
Number of cells.....	0	28	92	322	87	70	1	6.1005

TABLE 2

2000 cells from five median sections from different sclerotia

Number of sides....	3	4	5	6	7	8	9	average
Number of cells.....	0	126	283	1141	248	201	1	6.059

TABLE 3

2000 cells from five median sections cut perpendicular to those of table 2

Number of sides....	3	4	5	6	7	8	9	average
Number of cells.....	0	131	291	1136	259	183	0	6.036

In section the cells average more nearly six sides than do cork cells as reported by Lewis (1928), and their walls meet in groups of three and at 120° angles. They thus conform to the well-known principle of minimal areas, and tend to become as nearly spherical as is consistent with the contact, pressure, and adhesion of adjacent cells. Measurements of the angles were made with a protractor, for convenience as well as accuracy from photographs, in the manner described by Harper (1916) for *Pediastrum*. The constancy with which the exactly 120° angles are present and the regularity with which the walls meet in three is striking. Here and there quadrilateral faces with 90° angles are encountered, but this is to be expected in tetrakaidecahedral cells. Lewis stated that, 'If, on the average, the cells are hexagonal both in transverse and vertical section, nothing in biology is easier than to prove that their average number of contacts with surrounding cells is fourteen,' and the forms which will stack without voids and give a maximum volume with minimal area have been shown to be the tetrakaidecahedra of Lord Kelvin. It is obvious from casual inspection, as well as from the statistical evidence given in

the tables, that the cells just described have an average of approximately six sides in every plane and have, therefore, an average of fourteen faces. On the basis of the facts presented, which conform to Lewis' requirements for the tetrakaidecahedron, it appears that the pseudoparenchymatous cells of fungi also tend to be typically of this shape.

In figures 1 and 4 I have selected cells whose outlines in section are six-sided. In figure 1 are shown six cells *a*, *b*, *c*, *d*, *e*, and *f* surrounding a hexagonal cell which is slightly flattened, and similarly the six-sided central cell in figure 4 is slightly flattened. A figure showing a perfect regular hexagon I have not been able to find, and possibly such a figure does not exist. A perfect type could hardly be expected in a tissue whose cells vary in size as much as those in the tissue studied, and this is perhaps true for all plants, but that they approximate this shape appears evident.

The sclerotia are too small to section in three planes and I have therefore reconstructed from three different sclerotia the figure shown in 6. In figure 6, section *a* is cut parallel to the substrate, *b* is at right angles to *a*, and *c* is cut at right angles to both *a* and *b*. Figures 1, 2, and 3 also are cut at right angles to one another. Figure 1 is parallel to the substrate, 2 is at right angles to 1, and 3 is at right angles to 1 and 2. In all six figures the cells are nearly alike in outline, regardless of the plane of section.

Many pseudoparenchyma tissues even in the mature stage tend to indicate their plectenchymatous origin. The cells of the walls of ascocarps and pycnidia are not sufficiently voluminous to afford uniform mechanical pressures between the cells, and hence the latter are rarely isodiametric. In scerotia such as the one described above the fungous cells are under practically the same physical conditions as are the massed cells in higher plants and animals. The accompanying photographs (figs. 1, 2, and 3) might well be taken of elder pith, so close is the resemblance in form.

The histogenetic processes in the development of pseudoparenchymatous structures involve a symphyogenetic growth (Hein, 1927), which through septation, interhyphal contacts, and pressures, forms a tissue which is often identical in appearance with a true parenchyma of meristogenetic growth.

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Description of plate 3

Fig. 1. Part of section through sclerotium cut perpendicular to the substrate. Cells are approximately alike in size, form, and in mostly 120° angles.

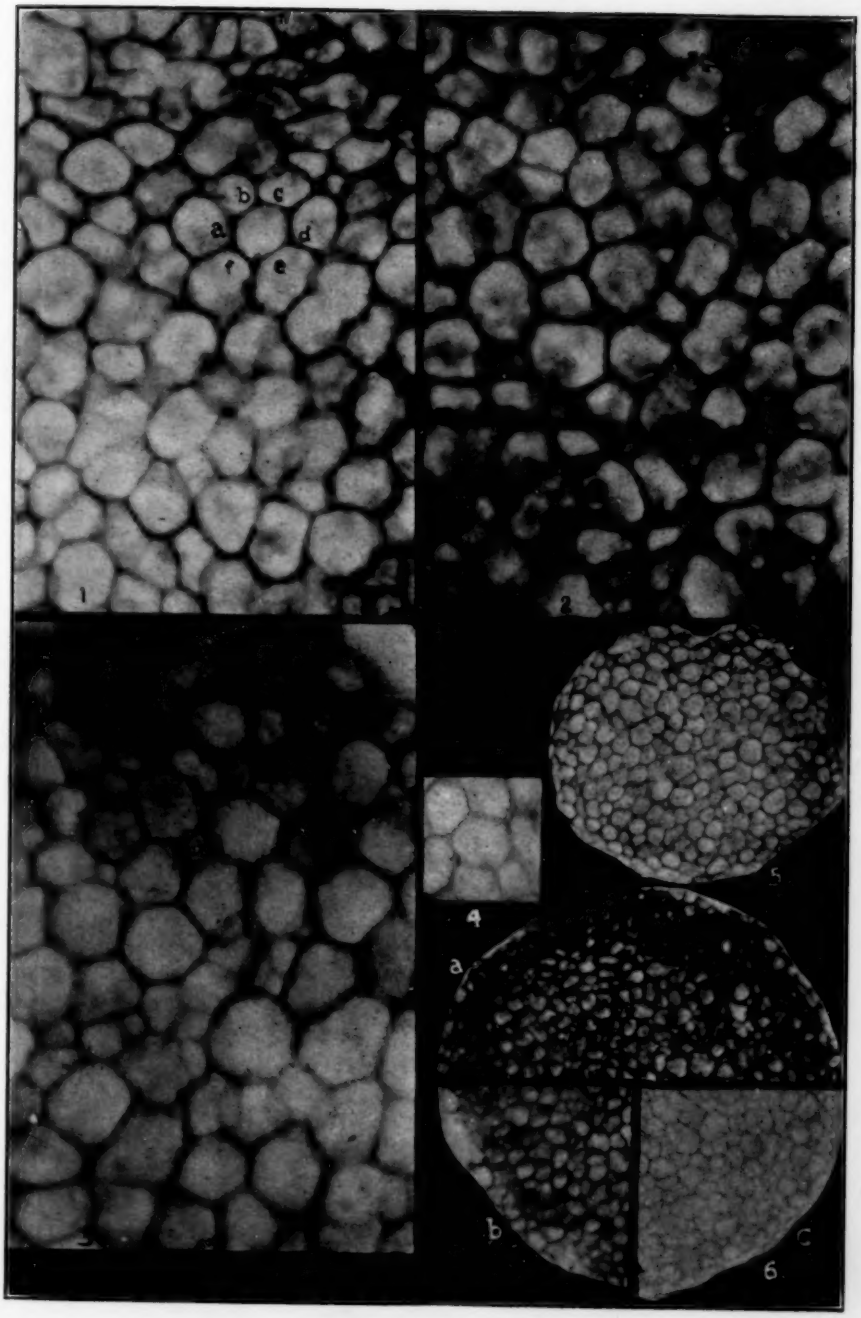
Fig. 2. A section similar to that of figure 1, but cut at right angles to it.

Fig. 3. A section similar to the above, but cut at right angles to the planes of both figure 1 and figure 2.

Fig. 4. Nearly typical form. The figure is surrounded by six cells but is a slightly flattened hexagon.

Fig. 5. The whole sclerotium in median section. It is nearly spherical in form.

Fig. 6. A figure constructed from three different sclerotia, with the sections cut in the three planes from one paraffin block, and put together to present the appearance that might be seen if they had been cut from a single sclerotium.



HEIN: TETRAKAIDECAHEDRON

Studies on the flora of northern South America—XIV
Melastomataceae from Colombia and Ecuador[1]

H. A. Gleason

Marcetia taxifolia (St. Hil.) DC. This species, which is rather widely distributed in southern Brazil, is also known from the Roraima region north of the Amazon. We now have it from Colombia, where it was collected by Woronow near the finca Francia, in the department of Huila.

Tibouchina oroensis n. sp. Stems shrubby, 2–5 m. high, the upper portion strongly 4-angled and appressed-hispid with brown hairs 0.4–0.7 mm. long, becoming subterete and nearly glabrous, the nodes subtended by a ring of tomentum, the internodes 1 dm. or more long; floriferous branches slender, spreading, 10–15 cm. long, the internodes 2–4 cm. long; petioles slender, 8–10 mm. long, densely appressed-setose; leaf-blades 5-nerved, thin, ovate, 20–35 mm. long, 15–18 mm. wide, short-acuminate, minutely appressed-serrulate with setose teeth, rounded to subcordate at base, conspicuously setose above with appressed yellow-brown hairs 1 mm. long and adnate for half their length, arranged in 2 or 3 rows between the veins, beneath hispid on the veins with free ascending hairs 0.7–0.8 mm. long and sparsely setose with similar hairs on the surface, veins impressed above, prominently elevated beneath, the veinlets obscure, reticulate; rameal leaves resembling the cauline but smaller and proportionately wider, the upper 10–18 mm. long by 8–15 mm. wide; flowers 5-merous, solitary in the upper axils and in terminal cymules of 3, on sparsely setose pedicels 2–3 mm. long, the lateral pedicels articulate to the end of sparsely setose peduncles 10–18 mm. long; hypanthium narrowly campanulate, 7 mm. long, 3.5 mm. in diameter as pressed, purplish-brown, obscurely 10-ribbed, marked with a transverse, sparsely setose line at the summit; sepals erect, persistent, broadly deltoid, united for 1 mm. at base, the free portion 1.5 mm. long, acuminate into a subulate tip 0.7 mm. long, membranous, glabrous on the back, closely and conspicuously ciliate with hairs 0.2–0.3 mm. long, the midvein prominently thickened; petals obovate, somewhat truncate, purple-blue, 2 cm. long; stamens 10, similar in shape; filaments slender, glabrous, equaling the anthers; anthers purple, linear-subulate, 8 or 9.5 mm. long, opening by a minute terminal pore; connective nearly 2 mm. long, bent anteriorly at right angles, inappendiculate, expanded at base into 2 anterior, bright yellow, subrotund protuberances about 0.8 mm. in diameter; ovary 5-locular, half-inferior, prolonged at the summit into 5 erect, flat, narrowly triangular, hispid appendages opposite the septa, surrounding the base of the style, 1.5–1.8 mm. long;

[1] Contributions from The New York Botanical Garden, No. 137

style filiform, 20 mm. long, slightly curved distally, minutely hirtellous below, glabrous above; stigma punctiform, not expanded.

Type, *Hitchcock 21,203*, collected between La Chorita and Portovelo, Prov. Oro, Ecuador, alt. 1000–2000 m., 28 Aug. 1923, and deposited in the United States National Herbarium (number 1,196,235; duplicate in herb. New York Botanical Garden). *T. oroensis* belongs to the section DIOTANTHERA and to the group of species numbered 140 to 151 in Cogniaux's monograph.

Monolena bracteata n. sp. Acaulescent, the leaves strictly basal; petioles slender, 25–30 mm. long, very minutely puberulent; leaf-blades lanceolate to oblong-lanceolate, membranous, dark green, 4–7 cm. long, 1.5–3 cm. wide, long-acuminate to an acute or obtuse apex, finely ciliate, rounded, truncate, or barely subcordate at base, 5-pli-nerved, or the larger with a faint additional basal pair, the secondaries few and obscure, about 6 mm. apart, glabrous on both surfaces, minutely puberulent on the primaries beneath; scape naked, slender, 5–9 cm. high, glabrous, 2-flowered, 2-bracted at the summit and with a single bract below each flower; bracts petaloid, very thin and translucent, obovate to obovate-elliptic, 12–14 mm. long, 8–10 mm. wide, sparsely veined, rounded at the summit; pedicels less than 1 mm. long; hypanthium broadly campanulate, 3.5 mm. long, glabrous, obscurely 10-ribbed; sepals 5, erect, broadly oblong, 2.5 mm. long, 2.1 mm. wide, rounded above, somewhat erose, glabrous, 3-nerved, very thin, separated by narrow sinuses; petals obovate, 9 mm. long, obtuse; filaments very thin and flat, 3 mm. long; anthers stout, obtuse, 2.1 mm. long, opening by a large ventro-terminal pore, the connective prolonged about 1 mm. at base and posteriorly tuberculate, bearing an anterior appendage 0.7 mm. long below the insertion of the filament; style very stout, thickened upwards, 4 mm. long; fruit broadly obconic, about 10 mm. in diameter.

Type, *Woronow & Juzepczuk 5844*, collected between Gabinete and Sucre, Caquetá Territory, Colombia, 9 July 1926, and deposited in the herbarium of the New York Botanical Garden. It is related to *M. cordifolia* Triana.

Leandra caquetensis n. sp. Stems freely and divaricately branched, 4-angled, densely strigose; petioles slender, 10–15 mm. long, strigose or somewhat hirsute; leaf-blades firm, ovate-lanceolate, as much as 9 cm. long by 3 cm. wide, sharply long-acuminate, finely ciliate, broadly cuneate at base, 5-nerved or obscurely 5-pli-nerved, the upper surface dark green, finely pubescent, especially on the primaries, the lower surface paler green, thinly sericeous; inflorescence a compact terminal panicle 4–6 cm. long, the axes strigose or sericeous, the nodes bearing small lanceolate bracts; flowers 4-merous, sessile in small terminal glomerules; hypanthium subhemispheric, 2.5 mm. long to the torus, densely hirsute with simple ascending hairs nearly 1 mm. long; calyx-tube not prolonged; sepals erect, ovate, 1.1 mm. long, acute, densely hirsute externally like the hypanthium,

the sinuses very narrow and the sepals contiguous; petals lanceolate-triangular, acute, 2 mm. long; filaments 2 mm. long, apparently jointed and somewhat inflexed at three-fourths of their length; anthers stoutly oblong, 1.2 mm. long, obtuse; connective thickened toward the base, prolonged 0.15 mm. and ending in 2 minute lobes on the sides of the filament; ovary wholly inferior, 4-celled, the summit glabrous, truncate; style slender, glabrous, 4.3 mm. long; stigma punctiform; ovules not appendaged.

Type, *Woronow & Juzepczuk 5909*, collected between Sucre and Cordoba, Caquetá Territory, Colombia, 11 July 1926, and deposited in the herbarium of the New York Botanical Garden. Its relationships within the genus are doubtful.

Killipia pedunculata n. sp. Arborescent, height not stated; stems glabrous, sharply quadrangular, the internodes 4–6 cm. long; petioles glabrous or minutely puberulent, flattened, 3–4 mm. long; leaf-blades firm, lanceolate or oblong-lanceolate, 7–9 cm. long, 19–23 mm. wide, acuminate, subrevolute, minutely and remotely setulose-serrulate (about 2–4 teeth per cm. of margin, 0.1 mm. long), broadly obtuse to subrotund at base, 3-nerved, with a faint additional submarginal pair, glabrous on both sides, the upper dark green and somewhat rugose, the lower pale green with finely reticulate veinlets; inflorescences in most of the axils, ascending; peduncles 15–30 mm. long; cymes trichotomously branched, about 9-flowered, with subulate bracts 1.5–3 mm. long at each node and at the base of each flower; flowers 5-merous; hypanthium campanulate, 3.8 mm. long to the sinuses, glabrous; calyx prolonged about 0.4 mm. beyond the torus, its lobes erect, broadly triangular, 1.6 mm. long, differentiated at the extreme apex into acute exterior teeth and obtuse or rounded, scarious sepals; petals broadly ovate, 4 mm. long, 2.7 mm. wide; stamens (immature) isomorphic, the anthers broadly oblong, the connective with a broad dorsal protuberance at base, the filaments gradually widened toward the base; ovary mostly inferior, 3-celled.

Type, *Killip 7771*, collected at 'La Gallera,' Micay Valley, Dept. El Cauca, 29–30 June 1922, and deposited in the herbarium of the New York Botanical Garden. It differs from *K. quadrangularis* Gleason in its more slender stem, the rounded leaf-bases, the pale under surface of the leaves, the much longer internodes and peduncles, the shorter and more slender petioles, the 9-flowered cymes, and the shorter bracts.

Miconia submacrophylla n. sp. Section TAMONEA: shrubby, the younger branches strongly flattened, very closely and thinly covered with brown, sublepidote tomentum, the internodes mostly 3–5 cm. long; petioles slender, 2–6 cm. long, thinly stellate-tomentose; leaf-blades unequal in each pair, narrowly oblong-elliptic, long-acuminate, finely dentate, rounded below to a subcordate base, 5-nerved with an additional obscure marginal pair, the primaries lightly impressed above, the secondaries broadly spreading, 3–5 mm. apart; upper surface bright green and glabrous, or minutely pubescent along the primaries near the base;

lower surface pale brown, closely but thinly covered with a sublepidote indument; larger leaves as much as 25 by 7 cm., the smaller of each pair about half as long as the larger; inflorescence a narrow terminal panicle, swollen at the nodes, with opposite branches, tomentose like the stem; flowers 6-merous, sessile; hypanthium obscurely 12-ribbed, campanulate, slighty constricted at the throat, 4 mm. long to the torus, gray with a very fine and close stellate tomentum; calyx-tube slightly flaring, 1.2 mm. long; sepals broadly triangular, 0.3 mm. long, 1.6 mm. wide; petals narrowly obovate, 7 mm. long, very obliquely truncate, attenuate to the base, stellate on the back; stamens dimorphic; large stamens: filaments subterete, softly villous, 7 mm. long; anthers subulate, 7 mm. long, the pollen-sacs prolonged at base into short lateral lobes, the connective into a swollen, basally truncate, unlobed, glabrous organ; small stamens: filaments subterete, softly villous, 6.5 mm. long; anthers subulate, 6.5 mm. long, the pollen-sacs prolonged at base into two short lateral lobes, the connective into two minute lateral lobes and one longer, rounded, projecting, dorsal lobe; ovary almost free, 5-celled, 12-ribbed, finely villous distally; style somewhat sigmoid, 11 mm. long, densely pubescent, the hairs varying from short and stellate at the base to long and villous at the summit; stigma truncate.

Type, *Woronow & Juzepczuk 6084*, collected at Hetuchá on the Rio Ortegueza, Caquetá Territory, Colombia, 20 July 1926, and deposited in the herbarium of the Botanical Garden at Leningrad. The aspect of the plant at once suggests *M. macrophylla* Triana, to which it is indeed closely related. Its leaves are much narrower than in that species and the structure of the anthers is quite different.

Miconia Voronovii n. sp. Section TAMONEA: branches stout, somewhat compressed, densely clothed with an indument of matted, brown, stalked, stellate hairs; petioles stout, angular, 5 cm. long, tomentose like the stem; leaf-blades firm, elliptic-ovate, as much as 28 by 16 cm., abruptly and sharply acuminate, obscurely serrulate with minute tomentose teeth, cordate at base, 7-nerved, the outer two pairs deflexed into the basal lobes and continued nearly or quite to the apex as marginal and submarginal primaries, the secondaries horizontal below, ascending at an angle of 70–80° above, averaging 7 mm. apart, the tertiaries prominently reticulate, all veins minutely impressed above, prominent beneath; upper surface dark green, finely stellate when young, nearly glabrous at maturity but persistently stellate along the primaries, especially toward the base; lower surface brownish green, softly and loosely stellate, the primaries pubescent like the stem; inflorescence a stout panicle 20 cm. long, its branches strongly but obtusely 4-angled, tomentose like the stem; flowers 7-merous, sessile; hypanthium cylindric-campanulate, 5.3 mm. long to the torus, thick-walled, densely and coarsely stellate-tomentose; calyx-tube somewhat flaring, 2.4 mm. long, tomentose like the hypanthium; sepals semicircular, 0.8 mm. long, stellate-tomentose on both sides; petals thick, obovate, 7.5 mm. long, 5 mm. wide, truncate or slightly obliquely retuse, reflexed-strigose on the back; filaments not yet fully expanded,

freely stellate-pubescent; small anthers subulate, 9 mm. long, the pollen-sacs divergent toward the base and prolonged dorsally into 2 rounded lobes, connective expanded dorsally at base into 2 ellipsoid adjacent elevated glandular-pubescent cushions, also glandular beneath; large anthers similar, 9.5 mm. long, the pollen-sacs abruptly divergent at base dorsally and laterally into 2 rounded lobes, the connective expanded at base dorsally into 2 ellipsoid oblique glandular-pubescent cushions which are confluent over the insertion of the filament; ovary nearly free, 4-celled, densely strigose; style straight, stout, 9 mm. long, villous with stellate hairs; stigma truncate.

Type, *Woronow & Juzepczuk 4529*, collected at Peñas Blancas, Dept. Antioquia, Colombia, 25 Apr. 1926, and deposited in the herbarium of the Botanical Garden at Leningrad. The species has leaves strongly resembling those of *M. macrophylla* (D. Don) Triana, but differs from it in pubescence and most remarkably in the character of the anthers.

Miconia titanophylla n. sp. Section ADENODESMA: stems stout, densely and coarsely tomentose with elongate hairs 3–4 mm. long and slightly branched at the end and with shorter hairs 1.5 mm. long bearing about 10 long radiating branches; petioles short (about 1 cm.) and mostly concealed, tomentose like the stem; leaf-blades membranous in texture, oblong-obovate, as much as 50 by 22 cm., abruptly short-acuminate, serrulate (teeth low, 4–9 per cm. of margin), gradually attenuate toward the base, which bears two obovate auricles, as much as 5 cm. long and overlapping across the petiole, 9–13-nerved, of which 5 and an obscure marginal pair traverse the blade proper, and the remainder enter the auricles; upper surface dark green and somewhat bullate, freely stellate when young, soon becoming glabrous, the midvein permanently stellate-tomentose; lower surface dull green and somewhat foveolate, sparsely but persistently stellate-pubescent on the veinlets, more densely so on the secondaries and primaries, and very densely tomentose on the midvein; lateral veins about 10 mm. apart, ascending at an angle of about 70°; inflorescence a short (11 cm.), freely branched, sessile panicle, densely tomentose like the stem; flowers nearly sessile, 5-merous; hypanthium and calyx narrowly campanulate, 8 mm. long, coarsely stellate-tomentose, the sepals broadly triangular, subacute.

Type, *Woronow and Juzepczuk 5980*, collected at Venecia, near Esmeralda, Caquetá Territory, Colombia, 17 July 1926, and deposited in the herbarium of the New York Botanical Garden. Although the inflorescence is past maturity and floral structures are not available, it is clear that the species is related to *M. macrotis* (Griseb.) Cogn. In the latter species, the leaves are plane, longer acuminate, more heavily veined, and much less pubescent, while the stem, petioles, and inflorescence are covered with a very close or nearly velutinous indument of short stellate hairs.

Miconia nigricalyx n. sp. Section EUMICONIA: branches nearly terete, stout, densely tomentose with brown stellate hairs when young, glabrescent with age, the internodes 5–8 cm. long; petioles stout, about 1 cm.

long, tomentose like the stem; leaf-blades thin, elliptic-oblong, as much as 25 cm. long by half as wide, the uppermost about half as large, abruptyl short-acuminate or apiculate, entire, obtusely rounded toward the base but cuneately decurrent on the petiole for 5 mm., 5-nerved or barely 5-pli-nerved, the secondaries mostly 4–6 mm. apart, ascending at an angle of 70°, the veinlets reticulate, all veins obscure and lightly impressed above, prominent beneath; upper surface dark green, thinly stellate when young, glabrescent and finely punctate at maturity; lower surface pale green, permanently and loosely stellate-pubescent; inflorescence an ample, freely branched, spreading panicle, the elongated branches closely pubescent or subtomentose with stellate hairs; flowers 5-merous, sessile in glomerules; hypanthium narrowly campanulate, 2 mm. long to the torus, black, stellate-tomentose with white deciduous hairs; calyx-tube somewhat flaring, 0.3 mm. long; sepals minute, triangular, acute, deciduous at anthesis; petals narrowly obovate, obliquely retuse, 2.8 mm. long; stamens dimorphic; small stamens: filaments flat, 2.4 mm. long; anthers subulate, 2.2 mm. long; connective truncate at base on the back, but prolonged ventrally and backward into two short lobes; large stamens: filaments flat, 3 mm. long; anthers subulate, 3 mm. long; connective broadened toward the base and nearly surrounding the filament, the lateral lobes obscurely developed, the dorsal broadly and obtusely triangular; ovary 3-celled; style straight, glabrous, 6 mm. long, the stigma truncate and barely expanded.

Type *Juzepczuk 4465*, collected at Peñas Blancas, Dept. Antioquia, Colombia, 24 Apr. 1926, and deposited in the herbarium of the New York Botanical Garden. It is most closely related to *M. rhytidophylla* Naud., which has much narrower leaves obtuse at base, smaller flowers, obtuse sepals, and more or less glandular pubescence in the inflorescence.

Miconia trichophora n. sp. Section EUMICONIA: shrubby, 1–2.5 m. high; branches slender with elongate internodes, stellate-pubescent and also sparsely glandular with spreading hairs 0.4–0.8 mm. long, the younger internodes tomentose, the older with scattered hairs; petioles slender, sparsely pubescent like the stem, 3–9 cm. long, those of the same pair of leaves sometimes very unequal; leaf-blades membranous, ovate-lanceolate, as much as 18 by 7.5 cm., acuminate to a blunt tip, conspicuously crenate, rounded or subcordate at base, 5-pli-nerved, with an additional pair close to and following the contour of the margin, the secondaries obscure above, prominent beneath, spreading at nearly right angles, 3–5 mm. apart, the tertiaries reticulate beneath; upper surface permanently pubescent with simple, spreading, yellow, crooked or curled hairs 0.5–0.8 mm. long and 0.8–1.1 mm. apart; lower surface sparsely puberulent with sessile stellate hairs, the primaries with stalked stellate hairs; panicle about 10 cm. long, open, few-flowered, its axes densely stellate-pubescent and glandular-hirsute, the lower nodes bearing spreading branches 2–3 cm. long, the middle nodes with sessile glomerules, and the main axis and its branches all with terminal glomerules of several sessile 5-merous flowers closely subtended by rounded appressed bracts; hypanthium campanulate, 3.7

mm. long to the torus, densely pubescent with spreading or ascending, crooked, hyaline, glandular hairs 0.5–0.8 mm. long and stellate-pubescent beneath them; calyx-tube prolonged 0.5 mm., somewhat spreading; sepals widely spreading or recurved, broadly round-ovate, membranous and veiny, thinly hirsute, strongly ciliate, projecting nearly 2 mm. beyond the exterior teeth, which are fleshy, broadly conic, strongly spreading, pubescent like the hypanthium, 1.2 mm. long; petals obovate from a broad base, 4.7 mm. long, 3.5 mm. wide, spreading, veiny, slightly retuse; stamens isomorphic; filaments linear, flattened, 3.6 mm. long; anthers stoutly linear-subulate, slightly retrorsely curved, 3.2 mm. long, the connective neither prolonged nor appendaged, but with a slight dorsal protuberance near the base; ovary 5-celled, half inferior, the free summit truncate-conic, 10-ribbed, bearing a terminal ring of glandular hairs as much as 0.4 mm. long; style subulate, 6 mm. long; stigma punctiform.

Type, *Killip & Smith 14,848*, collected in dense forest at 'Kilometer 16,' between Puerto Wilches and Puerto Santos, Dept. Santander, Colombia, alt. 110–115 m., 29 Nov. 1926, and deposited in the herbarium of the New York Botanical Garden. Field notes indicate that the petals are pink, the stamens and style white, and the fruit blue. *M. trichophora* is closely related, as shown by its stamens and pubescence as well as by its general habit, to *M. campestris* (Benth.) Triana and *M. biglomerata* (Bonpl.) DC. Both of these are Amazonian species, and it is noteworthy that the type locality yielded a considerable number of other species common in the Guianas and typically Amazonian in their relations. In these species the pubescence is much heavier, the leaves are stellate-pubescent above, the hypanthial hairs are shorter, and the ovary lacks the terminal ring of glandular hairs.

Miconia paspaloides n.sp. Section EUMICONIA: branches strongly 4-angled or nearly 4-winged, closely and minutely sublepidote-furfuraceous, the upper internodes 2 cm. long, the nodes surrounded and the leaves subtended by an elevated annulus; petioles stout, channeled above. 2–3 mm. long, pubescent like the stem; leaf-blades thin, narrowly obovate, the largest 20 by 7 cm., abruptly and sharply acuminate, entire, gradually narrowed from above the middle to a cuneate base, 3-pli-nerved, with an additional obscure marginal pair, the primaries lightly impressed above, prominent beneath, the secondaries about 8–13 mm. apart, slightly curved, ascending at an angle of 60–70°; both surfaces very minutely and sparsely stellate-puberulent, the venation beneath more densely so; inflorescence a narrow panicle, pubescent like the stem, its peduncle 5 cm. long, its branches 15 mm. below to 5 mm. above apart, 10–15 mm. long, simple or once branched; flowers 5-merous, sessile, crowded, secund, subtended by short, broadly ovate, stellate bracts; hypanthium campanulate, 2 mm. long to the torus, minutely stellate with sessile gray hairs less than 0.1 mm. in spread; calyx-tube nearly erect, prolonged 0.5 mm.; sepals reduced to 5 minute conic teeth less than 0.1 mm. long, separated by flat sinuses; petals broadly obovate, 2.3 mm. long, 1.7 mm. wide, rounded

at the summit; stamens essentially isomorphic; filaments flat, 2 mm. long (perhaps not fully expanded); anthers linear, 2.7 mm. long, opening by a broad terminal pore; connective prolonged straight back 0.6 mm., channeled on the ventral side, minutely dilated at the base; ovary half-inferior, subglobose, glabrous, strongly retuse around the style-base, 3-celled; style stout, 3.5 mm. long; stigma truncate.

Type, *Woronow & Juzepczuk 6436*, collected between Santa Marta and Marsella, Caquetá Territory, Colombia, 6 Aug. 1926, and deposited in the herbarium of the Botanical Garden at Leningrad. It is a member of the *Seriatiflorae* group, resembling *M. scorpioides* (Schl. & Cham.) Naud. in general habit, but differing in its 3-celled ovary and several other structural details.

Miconia Alberti n. sp. Section AMBLYARRHENA: shrub or small tree, 2–6 m. high; branches conspicuously and often sharply 4-angled, densely brown-furfuraceous-tomentulose above; petioles 4–10 mm. long, pubescent like the stem; leaf-blades lanceolate, as much as 15 by 3.5 cm., long-acuminate, entire, cuneate to the base, 5-pli-nerved, the outer primaries submarginal, the secondaries obscure above, spreading at nearly right angles; upper surface glabrous; lower surface thinly brown-furfuraceous along the primaries and some of the secondaries; panicle sessile or nearly so, freely branched, many-flowered, densely tomentulose, its axes sharply angled; flowers 4-merous, sessile in small glomerules of 3–5; hypanthium campanulate, 3.6 mm. long, very sparsely pulverulent or glabrate; calyx-tube prolonged 0.4 mm.; sepals 0.6 mm. long, broadly rounded, thin but fleshy in texture, equaled or barely exceeded by the triangular acute external teeth; petals pink, elliptic, 3.9 mm. long, 2.4 mm. wide, obtuse, reflexed at anthesis; stamens isomorphic; filaments 3.4 mm. long, the basal 3 mm. flattened, 0.4 mm. wide, slightly convex toward the inner side, the distal 0.4 mm. abruptly bent introrsely; anthers ovate-oblong, 2.2 mm. long, 0.7 mm. thick (radially), 0.8 mm. wide, opening by a minute terminal pore, the connective neither appendaged nor prolonged; ovary mostly inferior, its conical summit radially 8-winged; style slender, straight, glabrous, 7 mm. long, the stigma punctiform.

Type, *Killip & Smith 15,896*, collected in the vicinity of Las Vegas, Dept. Santander, Colombia, alt. 2600–3000 m., 21–23 Dec. 1926, and deposited in the herbarium of the New York Botanical Garden; two fruiting specimens from Norte de Santander, *Killip & Smith 20,028* and *20,566*, are also referred here. The ovary is apparently 4-celled. *M. Alberti* is related to *M. ulmarioides* Naud., which is less pubescent throughout with proportionately wider leaves shining above, rounded at base, and on longer petioles.

Miconia erosa n. sp. Section AMBLYARRHENA: upper internodes 6 cm. long; petioles and stem densely short-pubescent with purplish hairs and sparse erect glandular hairs 0.3 mm. long; petioles 3–5 cm. long, unequal in each pair; leaf-blades membranous, narrowly cordate-ovate, as much as

13 by 6.5 cm., long-acuminate, conspicuously and very irregularly erose-dentate, cordate at base, 7-nerved; upper surface velvety green, very finely pubescent with erect, substellate hairs and with scattered stout purplish hairs, 0.6–0.8 mm. long and at first glandular; lower surface softly and finely pubescent with similar but somewhat longer hairs, denser along the veins, where they are often purplish; panicle few-flowered, 10 cm. long, pubescent like the stem; flowers 7-merous; hypanthium campanulate, 3.2 mm. long to the staminal torus, pubescent like the stem, the walls thick and fleshy; calyx-tube prolonged about 1 mm., slightly spreading; sepals broadly depressed-semicircular, 0.8 mm. long, 2.2 mm. wide, finely pubescent within and without; exterior teeth recurved or spreading, stoutly subulate, 1 mm. long, pubescent like the stem, leaving a free margin of the sepals 0.4 mm. wide; staminal torus sparsely glandular with scattered erect hairs 0.2 mm. long; petals broadly cordate-obovate, retuse, 5.3 mm. long, the distal margin minutely erose-denticulate; stamens 14, isomorphic; filaments clavate-flattened, 2.5 mm. long; anthers oblong, 2.4 mm. long, the broad connective slightly prolonged but unappendaged; ovary completely inferior, 7-celled, the summit concave; style very stout, straight, 5 mm. long; stigma capitate.

Type, *Toro 1139*, collected at Dauro, Dept. Choco, Colombia, 6 Apr. 1928, and deposited in the herbarium of the New York Botanical Garden. It is related to *M. stricta* Cogn., which has more finely denticulate leaves, tomentose pubescence, shorter petioles and pedicels, longer styles, and 20–25 stamens.

Miconia spatellophora n. sp. Section AMBLYARRHENA: stems woody, terete, floccose with a dark brown tomentum, the internodes 15–30 mm. long; petioles stout, 4–5 mm. long, pubescent like the stem; leaf-blades firm, dull green, elliptic-oblong, 50–65 mm. long, 18–25 mm. wide, abruptly narrowed above to a linear, obtuse tip about 8 mm. long, entire, obtuse or subrotund at base, 5-nerved with an additional obscure marginal pair, the middle three primaries approximate above and extending through the narrow tip, the secondaries broadly spreading, inconspicuous, about 2 mm. apart, the veinlets obscurely reticulate; upper surface pulverulent when young, soon becoming glabrous; lower surface minutely puberulent on all the veins and veinlets; inflorescence a short and broad, freely branched panicle 4 cm. long, thinly stellate-pubescent; flowers 5-merous, sessile or minutely pedicelled; hypanthium campanulate, 10-ribbed, 1.8 mm. long, minutely and sparsely puberulent with substellate hairs; calyx-tube erect, prolonged 0.2 mm.; sepals broadly triangular, 0.2 mm. long, acute, their concave sides continued into the concave sinuses, the external teeth reduced to minute thickenings at the apex; petals suborbicular, 1 mm. long; filaments thick and flat at base, becoming narrower above, 1.5 mm. long, slightly bent at three-fourths of their length; anthers isomorphic, slenderly oblong, obtuse, 1.5 mm. long, with simple connective; ovary very short, half-inferior, with rounded summit; style straight, glabrous, 4 mm. long; stigma truncate.

Type, *Juzepczuk 6640*, collected at Gabineta, Dept. Huila, Colombia, 23 Aug. 1926, and deposited in the herbarium of the Botanical Garden at Leningrad. The species is probably related to *M. obovata* Triana.

Miconia brachygyna n. sp. Section CREMANIUM: shrubby, 3–4 m. high; younger branches essentially glabrous, short-setose at the nodes, shallowly sulcate with four rounded angles; petioles slender, 15–20 mm. long, pulverulent dorsally near the summit, otherwise glabrous; leaf-blades thin, bright green above, somewhat paler beneath, narrowly elliptic-oblong, as much as 16 by 4.5 cm., broadest near the middle, acuminate, cuneate or acute at base, entire, minutely and remotely spinulose-ciliate, 3-nerved with an obscure additional marginal pair, the second and third primaries about 5 mm. from the margin, secondaries strongly curved-ascending, prominent but scarcely elevated on either side, tertiaries conspicuously reticulate; upper surface glabrous; lower surface very minutely and sparsely puberulent, the hairs about 0.02 mm. long; panicle almost sessile, freely branched, 8–10 cm. long by 6–8 cm. wide, glabrous except at the nodes; bracts oblong-oblanceolate, 1 mm. long, soon deciduous; pedicels 0.4–0.6 mm. long; hypanthium subglobose, 1.3 mm. long to the sinuses, glabrous, freely punctate, as are also the pedicels; calyx-tube prolonged 0.3 mm.; sepals semicircular, 0.45 mm. long, the external teeth equaling them and broadly triangular; petals 5, obovate-oblong, 1.4 mm. long, slightly retuse; filaments slender, 1.7 mm. long, the basal two-thirds thickened and flattened, the distal third slender and terete; anthers obovate-oblong, 1 mm. long, the pollen-sacs 0.65 mm. long, opening by two wide terminal pores, the connective prolonged basally below the pollen-sacs into a large dorsal protuberance and two obscure ventral lobes; ovary half-inferior, apparently 3-celled, rounded at the summit; style terete, 0.5 mm. long; stigma truncate, not enlarged.

Type, *Killip & Smith 15,266*, collected on the Mesa de los Santos, Dept. Santander, Colombia, alt. 1500 m., 11–15 Dec. 1926, and deposited in the herbarium of the New York Botanical Garden. It is one of a group of four closely related species in Colombia, *M. Lehmannii* Cogn., *M. minuta* Gleason, and *M. mimica* Gleason being the other three. Of these *M. minuta* has a similarly short style, but is smaller in all its dimensions and conspicuously pubescent throughout the panicle. In comparison with *M. mimica* or *M. Lehmannii*, our species has much shorter styles. The question of heterostyly is at once suggested, and it is possible that we are dealing with long-styled and short-styled forms of plants which may eventually be properly associated with each other, or for which the second type of flower may sometime be discovered.

Miconia pallida n. sp. Section CREMANIUM: shrubby, 1–5 m. tall, freely branched; branches nearly terete, closely ferruginous-tomentose when young, eventually glabrate; petioles slender, 6–12 mm. long, pulverulent; leaf-blades thin but firm, pale green or yellowish green, obovate-elliptic, 4–6 cm. long, 18–25 mm. wide, obtuse or subacute, slightly

revolute, entire or remotely and minutely spinulose-denticulate, narrowed to an acute base, 3-nerved, the primaries impressed above, prominent beneath, the secondaries obscure above, spreading at nearly right angles; upper surface glabrous; lower surface thinly and sparsely pulverulent with cinereous stellate hairs, the primaries marked by marginal bands of stellate tomentum; panicle sessile, compact, freely branched, 4–8 cm. long by half as wide, its axes tomentulose; pedicels pulverulent, 1 mm. long; flowers crowded, 5-merous; hypanthium hemispherical, 1.8 mm. long to the torus, pale green or nearly white, very thinly and minutely puberulent or nearly glabrous; calyx-tube prolonged about 0.3 mm.; sepals broadly triangular to semicircular, 0.2 mm. long, obtuse, the exterior teeth triangular, subacute, not projecting; petals white or greenish white, nearly orbicular, nearly 2 mm. long, often slightly retuse; stamens isomorphic; anthers obovate-oblong, 1.9 mm. long, minutely cordate at base on the anterior side, the connective neither prolonged nor appendaged; filaments 2.2 mm. long, the basal three-fourths strongly thickened; style terete, 3.3 mm. long; stigma capitate.

Type, *Killip & Smith 18,389*, collected on the eastern slope of the Páramo de las Coloradas, above La Baja, Dept. Santander, Colombia, alt. 3900 m., 27 Jan. 1927, and deposited in the herbarium of the New York Botanical Garden; other material in the same herbarium is *Killip & Smith 17,272*, *17,320*, *17,710*, *17,796*, and *18,180*, all from Santander, and two collections of Triana from near Bogota. The two latter specimens have been confused with *M. granulosa* (Bonpl.) Naud., to which *M. pallida* is apparently related. The former is distinguished by its much longer sepals and especially by its leaves, which are proportionately longer, more sharply acute, distinctly 3-pli-nerved with an obscure marginal pair besides, and densely brown-tomentose over the whole lower surface.

Tococa stellata n. sp. Young stems distinctly flattened, more or less sordidly pubescent in two opposite lines at each node or all around it, otherwise glabrous, the internodes 3–5 cm. long; leaves dimorphic; large leaves: free petioles 10–15 mm. long, sordid-pubescent on upper side; formicaria didymous, semiobovoid, glabrous, 20–25 mm. long, adjacent to the blade but below it; blades thin, lanceolate to oblong-lanceolate, as much as 9 by 25 cm., long-acuminate, obscurely denticulate and minutely ciliate, obtuse or subrotund at base, 5-nerved, primaries and secondaries lightly impressed above, prominent beneath, the latter 6–10 mm. apart, ascending at an angle of 70–80°, the tertiaries inconspicuous and reticulate; upper surface mostly glabrous, but short-setose toward the margin; lower surface very sparsely short-setose on the veins; small leaves: petioles 10 mm. long, with small (5 mm.) or no formicaria; blades as much as 5.5 by 13 cm., otherwise like the larger; inflorescence a narrow compact panicle, its branches strongly angular and freely short-setose; flowers 5-merous; hypanthium nearly cylindric, narrowly 5-winged, the wings densely hirsute with simple hairs, the sides glabrous; sepals in line with

the wings, depressed semicircular, the exterior teeth conical, not projecting, densely hirsute; ovary-summit conic, 10-ribbed, truncate and crowned with about 30 straight bristles 1 mm. long; style enlarged upward to the truncate stigma.

Type, *Woronow 6053*, collected at Corea, near Hetuchá, Caquetá Territory, Colombia, 20 Jul. 1926, and deposited in the herbarium of the Botanical Garden at Leningrad. It is a member of the section PTEROPHORAE and stands next to *T. stephanotricha* Naud., which differs in its densely hispid stem, petioles, and formicaria, its broader leaves setose above and rounded at base, and its glandular-hirsute hypanthium. The flowers of the type are very immature, so that dimensions have not been stated.

Myrmidone filiformis n. sp. Stems woody, when young conspicuously flattened and long-hirsute with hairs 5–7 mm. long and flattened at base, in age subterete and glabrescent; leaves dimorphic in each pair, the larger on petioles 2 cm. long, hirsute at base, the upper four fifths bearing a glabrous 2-lobed formicarium, the blades elliptic, membranous, as much as 15 cm. long by 7.5 cm. wide, abruptly acuminate, irregularly denticulate and conspicuously ciliate, essentially glabrous on both surfaces, 3-nerved with an obscure additional marginal pair, the primaries sparsely setose at the base beneath, the secondaries prominent beneath, spreading at an angle of about 75°, the tertiaries reticulate; smaller leaves on sparsely setose petioles 5 mm. long, without formicaria, the blades resembling the preceding but half as large; inflorescence a few (3–5)-flowered axillary raceme, 1–2 cm. long, in most of the upper axils, the axes minutely puberulent; pedicels 10–15 mm. long, slender, jointed and minutely bibracteolate 1.5 mm. from the summit; flowers 6-merous; hypanthium obconic, 5 mm. long to the torus, minutely puberulent at base, marked with minute scattered verrucosities; calyx-tube somewhat flaring, 1.1 mm. wide, glabrous; sepals broadly depressed-triangular from acute sinuses, apiculate, 1.1 mm. long, the external teeth adnate almost to the tip of the sepal, filiform, spreading or often reflexed, 9–10 mm. long; petals rather thick, elliptic, broadly obtuse, 8 mm. long, 5 mm. wide; stamens isomorphic, the filaments flattened; anthers as in *Tococa*, radially flattened, the connective thickened basally and bearing a small hollow dorsal protuberance; ovary chiefly inferior, the summit glabrous, 12-ribbed, terminated by a 6-ribbed beak 2 mm. long and erose at the apex, 4-celled; style 9 mm. long, stout, gradually thickened upward; stigma dilated.

Type, *Woronow and Juzepczuk 6421*, collected between Santa Marta and Marsella, Caquetá Territory, Colombia, 4 Aug. 1926, and deposited in the herbarium of the Botanical Garden at Leningrad. Aside from the axillary clusters and 6-merous flowers, which place the plant in *Myrmidone*, it has the general habit of a *Tococa*. The other species of *Myrmidone* have pli-nerved leaves, formicaria adnate to the blade, nearly sessile flowers, and much shorter external teeth.

Blakea argentea n. sp. Branches obscurely quadrangular and 4-sulcate above, soon becoming subterete, the youngest densely furfuraceous-tomentulose, the older glabrous, the nodes strongly swollen; petioles slender, 10–18 mm. long, tomentulose like the stem when young, eventually glabrous; leaf-blades subcoriaceous, elliptic, the largest 95 by 37 mm., abruptly acuminate into a cusp 3–4 mm. long, broadly cuneate at base, 5-nerved, the outer pair obscure; upper surface dull green, glabrous, densely punctate; lower surface at first cinereous, later silvery with a thin but very close persistent tomentum; flowers 6-merous, in fascicles of 2–4 in the upper axils; pedicels tomentulose like the petioles, eventually glabrous, 15–20 mm. long; bracts 4, essentially free, broadly ovate oblong, 8 mm. long, thinly tomentulose; hypanthium at anthesis 1 mm. longer than the bracts, very sparsely pulverulent; calyx calyptriform, ovoid, sparsely tomentulose, deciduous at anthesis; petals broadly rhomboid, before anthesis 5 mm. long; filaments narrowly triangular, tangentially flattened, nearly 1 mm. wide at base; anthers tangentially flattened, narrowly oblong, obtuse, the pollen-sacs somewhat prolonged at the base; connective stout, prolonged at base into a short dorsal spur; ovary inferior, its summit 6-ribbed, conic, closely surrounding the style-base, the latter immersed 2.5 mm. and 2 mm. in diameter; style stout, truncate.

Type, *Toro 1255*, collected at Salgar, near Medellín, Colombia, 20 July 1928, and deposited in the herbarium of the New York Botanical Garden. No fully expanded flowers are available, but one past maturity shows that the anthers are only 3.5 mm. long and the style about 6 mm., a third of which is enclosed by the ovary. *B. argentea* is related to *B. caudata* Triana, *B. rostrata* Berg, and *B. brachyura* Gleason, and is distinguished from all of them by the silvery tomentum on the leaves, as well as by other characters.

INDEX TO AMERICAN BOTANICAL LITERATURE
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The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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